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Aquatic Sciences

Overview Article

Species diversity of the Okavango Delta, Botswana

Lars Ramberg[1,*], Peter Hancock[2], Markus Lindholm[3], Thoralf Meyer[1], Susan Ringrose[1], Jan Sliva[4], Jo Van As[5] and Cornelis VanderPost[1]

[1] Harry Oppenheimer Okavango Research Centre, University of Botswana, P. Bag 285, Maun, Botswana
[2] Ecotourism Services, Maun, Botswana
[3] Department of Biology, University of Oslo, Norway
[4] Munich Technical University, Munich, Germany
[5] Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa

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Abstract. In the Okavango Delta (about 28,000 km^2) the number of identified species is 1,300 for plants, 71 for fish, 33 for amphibians, 64 for reptiles, 444 for birds, and 122 for mammals. The local occurrence of different species of these taxonomic groups in the Okavango Delta is mainly due to a hydrological gradient from permanent streams and swamps to seasonal floodplains, riparian woodlands, and dry woodlands. This level of species diversity is normal for the southern African region, and all analyzed aquatic groups are composed of ubiquitous species with an additional significant proportion of species originating from northern, more tropical systems. Cyclical variations in climate over thousands of years have created a huge wetland complex in the upper Zambezi and Okavango Rivers during wet phases. This wetland complex has fragmented into the Okavango Delta and other large wetlands in Zambia during dry phases. There are no endemic species in the Okavango Delta while the South-central African wetland complex is a centre of endemism. Species diversity of the Okavango Delta is a consequence of this unique environment, with dynamic shifts in flooding patterns that in turn force constant changes in patterns of plant succession and dependent animals. Temporal variations in flooding also cause accumulation and sudden mobilization of nutrients which are readily used by well adapted plant species. As a consequence, locally high biological productivity occurs, which in turn results in high numbers of grazing mammals.

Key words. Biodiversity; species; habitat; Africa; wetlands; Okavango.

Introduction

The Okavango Delta in northern Botswana has a large variety of aquatic, wetland and terrestrial habitats and the rich typical African bird life and wildlife and its pristine beauty enthrall anybody visiting it. It is often said that its biodiversity is "high" but the opposite statement is also common; that it is "normal" or "low" for the Southern African region. However, there have been no systematic attempts to analyze Okavango Delta biodiversity, the factors that are causing and regulating it, and this is the first attempt to bring all available facts together.

Physical description

The Okavango River originates on the Angola highlands, flows through the Caprivi strip in Namibia and ends in the Okavango Delta or during wet periods in the large Makgadgadi saltpans in the Kalahari (Fig. 1). Due to low

* Corresponding author phone: +267 6861833; fax: +267 6861835; e-mail: lramberg@orc.ub.bw
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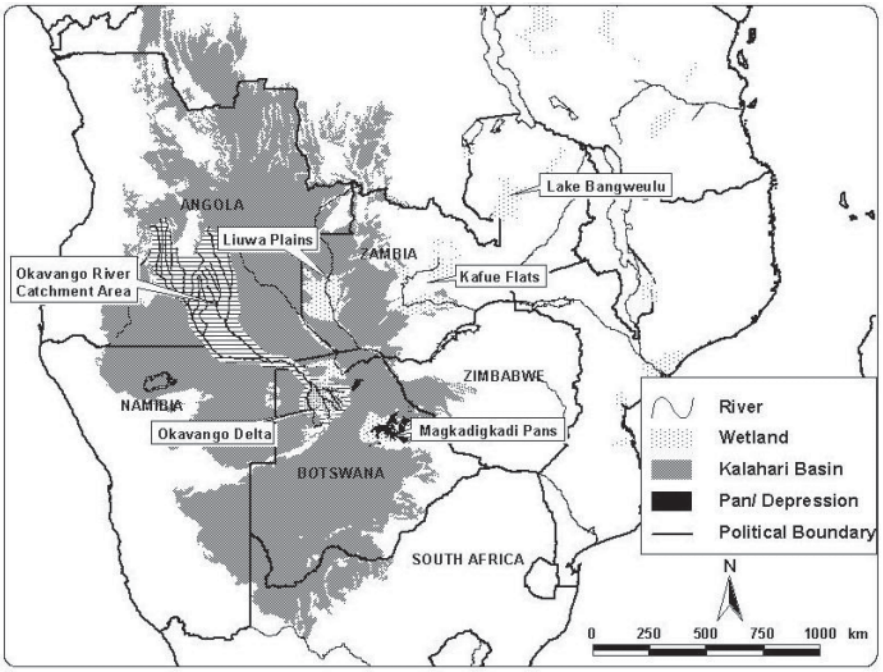

Figure 1. The location of the Okavango River Delta on the Southern African sub-continent with adjacent major rivers and wetlands. Note that the Okavango River basin is located almost entirely within the Kalahari (sand) Basin and that the river ends in a large salt pan, the Makgadikgadi. The river basin is shared by three states.

gradients the water that fell as rain in Angola in November arrives in the upper Delta (the Panhandle) around February–March and moves slowly as a huge wave across the wetland landscape until it reaches the distal parts in July. There is, however, another localized wet period caused by rains occurring in December–March. The Delta thus has two fairly predictable wet periods and is a typical flood-pulsed system usually with one flooding a year. However, during years of heavy rainfall over the Delta extensive flooding can already occur in January and continue until the second flood peak arrives in April–July. This has happened once during the eight years the Harry Oppenheimer Okavango Research Centre (HOORC) has been working in the Delta, when seasonal floodplains which were normally water covered for 3–6 months were continuously under water for about 12 months in the year 2000. In the upper permanently flooded parts of the Delta water level variations between and within years are usually small (Fig. 2), being less than one meter, while these variations in rivers in the seasonally flooded areas can be 1–2 m. The flooding of floodplains, which often are on a lower altitude than the feeding stream, usually takes the form of an overflow of river banks that function as thresholds. The maximum annual water level variations in the deepest parts of these seasonally flooded areas can be 3–4 m.

The mean annual inflow to the Delta is 9.2×10^9 m^3 and rainfall contributes an additional 6×10^9 m^3 (McCarthy and Ellery, 1998). Only 1.6% of this leaves the Delta as outflow through the Thamalakane River (Figs. 2 and 3). It is estimated that the loss through regional groundwater outflow is less than 2% and probably nothing (Gieske, 1995); consequently 96–98% of total inflow is lost through evapotranspiration within the Delta.

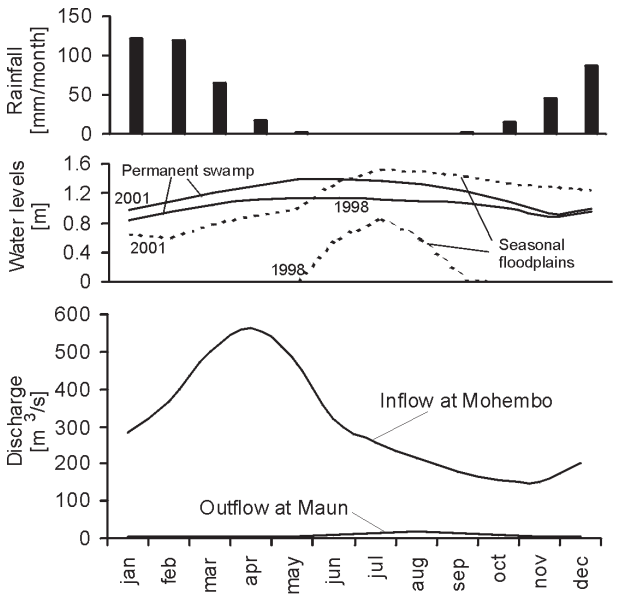

Figure 2. A. Mean annual rainfall in the Okavango Delta. B. Water level variations during two contrasting years, (dry 1998 and wet 2001) in the upper permanently flooded area, and in the Boro River in the seasonally flooded area. C. Inflow and outflow pattern.

The Delta has a typical continental climate with the highest daily maximum temperature of 34–35 °C in October and the lowest of 25 °C in July. For this month the mean minimum temperature during the night is however only 8 °C (Mendelsohn and el Obeid, 2004), frosts are locally common and thin ice forms occasionally on the shallow waters in the Delta. The mean annual rainfall is 460 mm in the south and 490 mm in the northern part of the Delta, and the evapotranspiration rate is about 1,500 mm (Dincer et al., 1987). As in other areas close to the tropics of Cancer and Capricorn the variations in rainfall between years are very large (Nicholson, 2000).

The Okavango Delta is located between a series of fault lines (Fig. 3) that form the southwestern extension of the East African Rift system (Cooke, 1980; Modisi et al., 2000). Seismic activity in this area started about 2.5 million years ago, which is also the approximate age of the Delta (Tiercelin, 2003). The area between the faults appears to have been subsiding and tilting through time causing the inflowing river to be un-confined laterally causing it to branch out in a number of dispersed distributaries (Fig. 3). Sediment transport in these has caused the deposition of an alluvial fan that is slightly conical and has a low gradient, 0.00036 along the main direction of flow (McCarthy et al., 1997).

The extent of alluvial deposition has varied widely over geological time and the palaeo-delta was two to three times larger than at present. This is caused by large swings in climate from very wet periods to dry ones (Tyson et al., 2002). The development of the present delta-fan appears to have been preceded by an extensive dry period with east-west sand dune formation, whose reworked sediment has contributed largely to the delta sands (Stokes et al., 1997; Ringrose et al., 2002). The actual size of the Okavango Delta is very much a matter of definition and large differences in size can be noted between authors. Gumbricht et al. (2004) used images taken during the last 30 years and gave as a summary for this period the total area flooded at least every decade to 14,000 km^2, of which 9,000 km^2 is actual wetland, the rest being islands. The total areas of the "Okavango wetland" are given as panhandle: 820 km^2, permanent swamp: 2,500 km^2, seasonal swamp: 3,300 km^2 and occasional swamp (flooded at least each 10th year) to 7,100 km^2. Permanently dry areas not included in this classification forming islands or peninsulas are about 4,000 to 10,000 km^2. By including these areas and areas that have been flooded during historical times (1850-present) (Fig. 3), the total area of the Okavango Delta thus defined is 28,000 km^2.

The major swings in Delta size appear to have been due to a combination of climatic changes and tectonic shifts brought about by faultline reactivation. Evidence from old floodplains suggest that early alluvial fans may have been fed from the Kwando and now ephemeral rivers to the west, while later fans accumulated from a pre-Okavango system and were deposited along a north easterly and south easterly trends in the the Magkadigkadi-Okavango-Zambezi (MOZ) basin (Ringrose et al., 2002). A system resembling the present Okavango probably developed over the last 40,000 years, as a result of movement along the Thamalakane and Kunyere faults (Ringrose et al., 2005). Intervening fluctuating years of high and low rainfalls were prevalent but difficult to track because of "anti-phase" conditions in the Delta (Huntsman-Mapila, 2005). A wet period appears to have been prevalent during the regionally dry Late Glacial Maximum (Partridge et al., 1997; 1999). Periods of high flow interspersed with low flow conditions through the Okavango system 13,000–14,000 years ago, and intermittent seasonal flow occurred 6,300 years ago. This was probably the last time when all the major distributaries were fully flooded. By this time the major pattern of rivers, large peninsulas and islands was formed thereby providing geomorphic controls for the landscape diversity present today (Anderson et al., 2003).

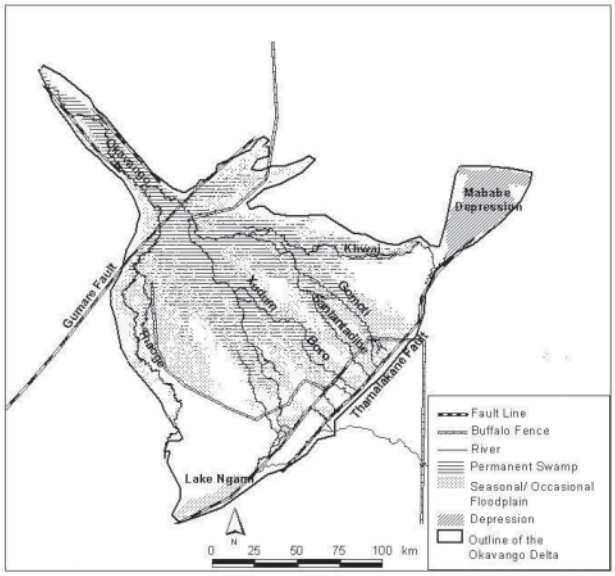

Figure 3. The Okavango Delta with major fault lines; major streams; distribution of permanent swamps, seasonal and occasional grasslands and woodlands; and the buffalo fence. The total area is 28,000 km^2.

The geological history of the Zambezi and Okavango rivers, recently reviewed by Timberlake and Childes (2004), explains much of present biodiversity. There is both geological and biological evidence that the Okavango River and Delta has been directly hydrologically connected to the upper Zambezi and to the Kafue Rivers (Fig. 1) forming one of the major wetland systems throughout the MOZ basin (Ringrose et al., 2005). The link between the Zambezi and Makgadigadi seems to have been breached and re-established on a number of

occasions from about 0.7 million years BP possibly to as late as 400,000 years BP (Ringrose et al., 2005). The Kafue River was captured by the Middle Zambezi sometime in the mid or late Pleistocene, while its upper stretch with Lake Bangweulu became connected to the Congo River sometime during this time period.

The most important feature that makes the Delta unique is the extreme spatial and temporal variations in the flooding pattern, which change over at least four time scales. The longest is over geological periods and described above. Since around 1850 the flooding pattern has moved from a very westerly to a central and now a very easterly distribution (McCarthy and Ellery, 1998), with some recent evidence of a return to a westerly trend. There are dry and wet periods as well with about 8 and 18 years interval (Tyson et al., 2002), which causes the seasonally flooded areas to withdraw and expand. Finally the flooding pattern can change from year to year due to local factors such as vegetation blockages in the streams causing damming and overflow of riverbanks. Controls on recent changes to Delta ecosystems have been discussed by a number of authors and summarized in Ringrose et al. (2003a; 2005).

As mentioned above a mean 96–98% of inflowing water is lost as evapotranspiration in the Delta and the rest leaves through outflow systems, most commonly through the Thamalakene and Boteti Rivers (Figs. 1 and 3) which occasionally reach the final sink, the huge Makgadigadi saltpans in the Kalahari. Sometimes, however, outflow is also deviated to the lake depressions, Ngami and Mababe to southwest and northeast. This happens only during wetter years while during dry periods there is no outflow from the Delta. Almost all inflowing water and sediment comes from heavily weathered Archean and Proterozoic rocks, which are nutrient poor, hence the Delta sediments and soils are poor in nutrients (Huntsman-Mapila et al., 2005). The conductivity in the inlet is 40–50 µS/cm, total phosphorus 0.02–0.03 mg P/L and total nitrogen 0.36 mg N/L (Cronberg et al., 1996). These are typical levels for the streams in the Delta, while the seasonal floodplains have 5–10 times higher nutrient levels (Högberg et al., 2002). Very high nutrient levels can be found in isolated pools used by wallowing and drinking wildlife.

The Okavango Delta occurs within a massive shallow basin within the middle of southern Africa. The part of the depression filled with sands is called the Kalahari Basin (Fig. 1). In its southern sub-basin the Okavango River flows into the Delta and eventually into the Makgadikgadi Pans (Mendelsohn and el Obeid, 2004). Here there is a vegetation gradient mainly caused by very low rainfall in the south (200 mm in southern Botswana) to 1,200 mm in the north in central Angola-Zambia (Ringrose et al., 1999, 2003b). The vegetation belongs to the vast Sudano-Zambezian Region (Werger and Coetzee, 1978) characterized by woodlands and savannas and without any very distinct sub-divisions although taxonomic gradients occur in particular from south to north. White (1983) however, identified the "Zambezian Phytochoria" based on the number and proportion of endemic species, whose area predominantly includes the Okavango and Zambezi River basins. This "regional centre of endemism" (op. cit.) has a number of huge wetlands (Fig. 1) in its central part including the Okavango Delta that during the recent past have all been hydrologically connected to each other (Timberlake and Childes, 2004; Timberlake, 1998).

It should be noted that there are no permanent waters south of the Delta and the extensive area of dry Kalahari savanna has probably functioned as an effective barrier against migrations of aquatic organisms.

As the Delta is on the axis of the East African Rift, there is a strong possibility of early hominid migrations into the region up to several million years ago (Butzer, 1984). Indication of human life comes in the form of stone tools found in several places (Butzer, 1984; Thomas and Shaw, 1991) and produced between 200,000 up to 35,000 years ago (Butzer, 1984; Mendelson and el Obeid, 2004). Farming could have started as early as 2,000 years ago and most sites showing such evidence date from between 1,500 and 1,000 years ago. The Delta itself has been fairly well protected against farming and in particular against livestock by the tsetse fly (*Glossina morsitans*) that was abundant until recently. Early humans in the Delta were the San ("Bushmen") living as hunter-gatherers. They have now all left the Delta and are living in villages in the periphery. In terms of human occupancy tourist lodges and adjacent satellite villages for service personnel are now common features.

To keep the livestock away from the wildlife carrying diseases like the foot-and-mouth disease, a "buffalo fence" was constructed in 1982 (Fig. 3) that is fairly effective in closing off all wildlife movements between the Delta and areas to the west and south.

Habitat diversity

A mosaic-like vegetation pattern characterizes the Delta from permanent swamps, over a gradient of seasonally flooded types of swamps and grasslands to riverine woodlands and dry savannas that are never under water. The complex pattern is mainly caused by ever changing river courses and the growth of islands that in most cases seem to have started as termite mounds (McCarthy et al., 1998). There are about 150,000 islands in the Delta (Gumbricht et al., 2004) each with a typical vegetation zonation.

There are large variations in vegetation patterns over small distances, although the Delta is very flat and is made up of homogeneous sand (Fig. 4). In an intensely studied area in a central part of the Delta two transects

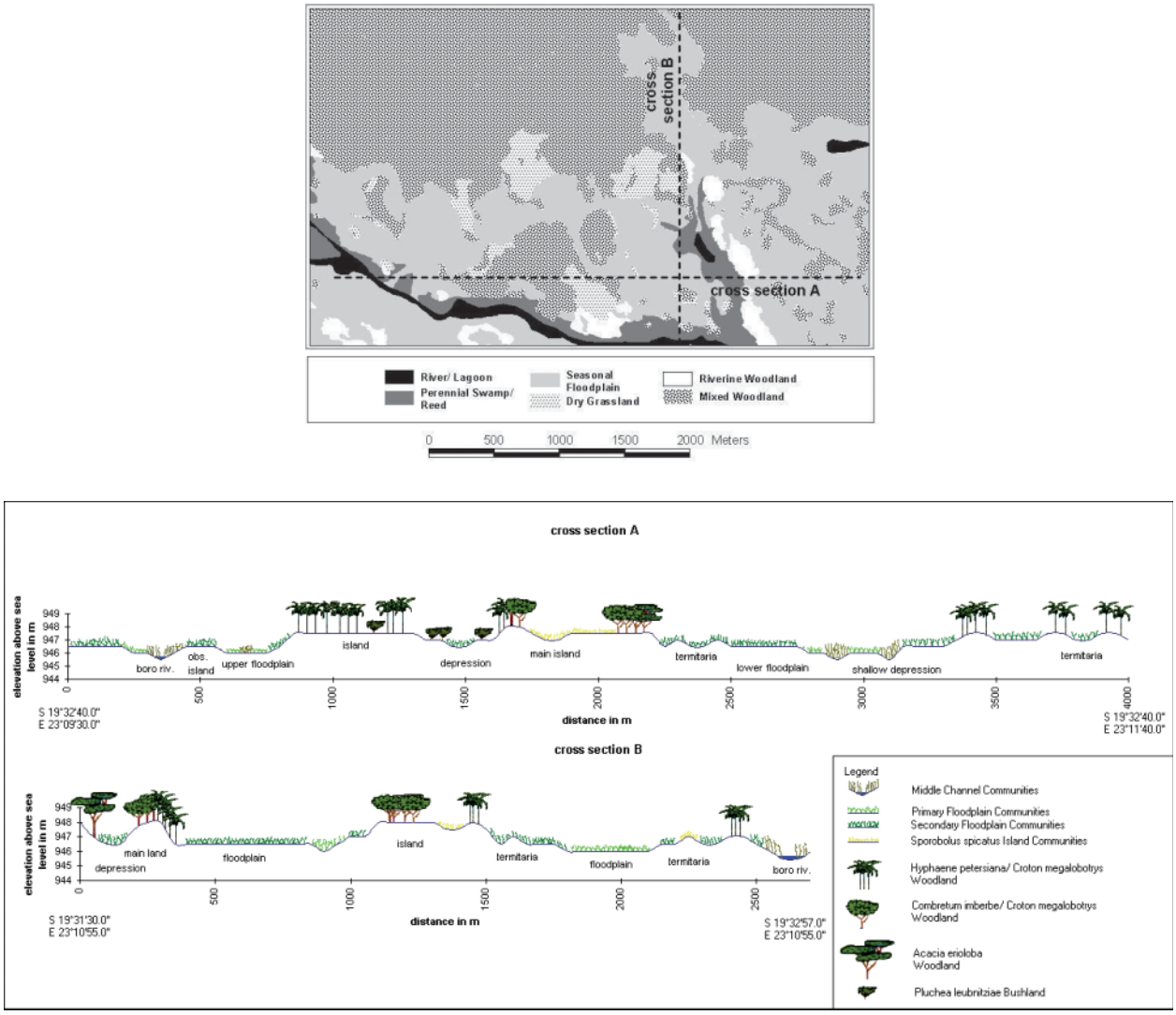

Figure 4. A. Detailed vegetation map of the HOORC research area in the central Okavango Delta with two inserted transects. B. Distribution of vegetation habitats along these two transects relative to elevation (Modified from Meyer, 1999).

4,000 m and 2,700 m long, respectively, had a maximum variation in elevation of two meters, but crossed vegetation types from permanent open water communities – sedge lands – grasslands – riverine woodlands – dry woodlands, and some of these habitats occurred several times along the same transect (Fig. 4). These small differences in elevation are making large differences in the frequency and duration of flooding, which causes the large variations in vegetation in a seemingly flat and homogeneous environment.

A vegetation/habitat map over the whole Ngamiland, 110,000 km^2, including the Okavango Delta of 28,000 km^2 was produced by HOORC 2001–02, based on Landsat images, air photos and a large number of ground-truth transects (502 transects of 90 or 100 m length). The classification of habitats was based on a combination of life form characters and dominant species. In total 46 habitats were identified. Landscape variety was then measured as suggested by the Corina Land use programme by recording the number of different habitats in 3 × 3 km squares (European Union, 2000).

The proportion of the Okavango Delta occupied by the dominant class "channels and recently inundated floodplains" is a fairly low 8.9 per cent (Table 1). As the dominant class occupies a small area in total, the other classes are likely to be abundant, but will occupy even smaller areas.

In the Delta study area the average polygon (i.e. specific habitat fragment) is fairly small being 0.05 km^2. The number of polygons per unit area, known as Monmo-

Table 1. Vegetation/Habitat characteristics in the Okavango Delta and surrounding Ngamiland.

	Delta	Rest of Ngamiland
Area in square km	26,662	81,245
Number of vegetation classes	45	46
Proportion of dominant class	8.9 %	9.0 %
Number of polygons	520,079	831,440
Average polygon size (m^2)	51,266	97,717

Dominant class in Ngamiland = Low open shrubbed grassland with sage bush.
Dominant class in Okavango Delta = Channels and recently inundated floodplains.

nier's (1982) fragmentation index, is on average 180 in a 9 km^2 quadrate. The number of different habitat types in these 9 km^2 areas varies between 1 and a maximum of 31. The distribution is skewed with clustering of cells in the 3–11 range and a heaping of frequencies occurs at values 5 and 6. Thus, the majority of 3×3 km cells contain 5 or 6 different vegetation classes. However, as there are as a mean 180 polygons in each of these cells it means that each habitat type is repeated 30–36 times in each cell. In the EU study (2000) the number of habitats per cell varied between a low of 2.4 in Austria to a high of 4.4 in Luxembourg. The average for the EU is 3.6, which again indicates that the habitat diversity as well as the habitat fragmentation is high in the Okavango Delta.

Figure 5 shows the resulting distribution of cells with varying degrees of habitat variety. The high variety zones along the edges of the Okavango Panhandle and Delta stand out and contrast with the lower degree of variety within the interior Delta and the dry lands further from the Delta. Of particular interest are the cells with exceptionally high vegetation variability (over 15 classes per cell). These are mostly located along the perimeter of the wet Delta, along the Panhandle, and along the major flow channels to the east and west (Fig. 3). These are areas, which tend to receive flooding at intermittent periods, i.e. they are not permanently flooded nor permanently unflooded areas. These areas with the least stable and predictable environments have thus the highest habitat diversity.

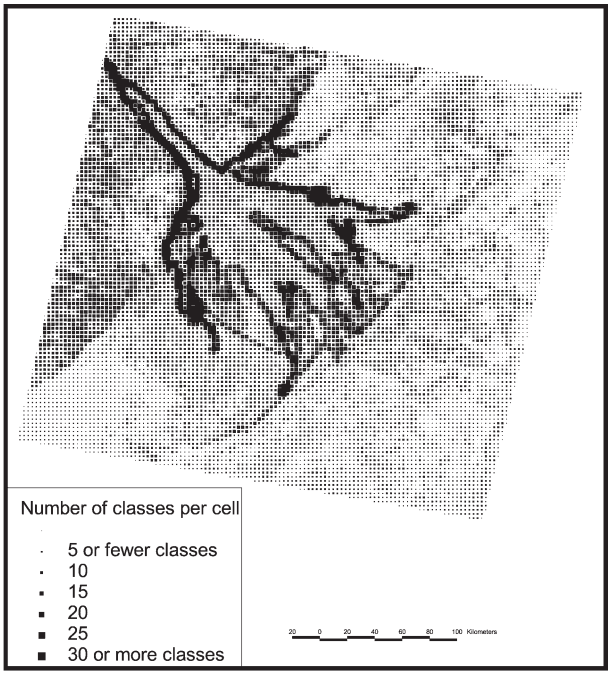

Figure 5. Number of habitats per 3×3 km squares in the Okavango Delta.

Biodiversity of different plant and animal groups

Algae

As far as we know no taxonomic study of Delta algae has been published. Cronberg et al. (1996) sampled rivers, floodplains and isolated pools during four occasions 1991–92 and used quantitative methods for the determination of the dominating species' biomass. In general rivers had very low biomass, below 1 mg/L fresh weight. Floodplains had a large variation in biomass with generally higher biomass than the rivers. In both habitats the Chlorophyceae contributed most species (total 23) followed by Cyanophyceae (9) and Bacillariophyceae (6). The total number of species was about 50. The isolated pools could have very high biomasses, particularly if they had been fertilized by dung from hippopotamus or drinking animals. Typical species here were the euglenophytes. In lagoons and pools the plankton succession is often interrupted by turbation from drinking and wallowing animals (Ramberg unpublished). Most species here are small Chlorophyceae and diatoms or good swimmers like *Cryptomonas* and *Peridinium*. In the very shallow waters in the vegetation there is a typical flora of colonial swimming forms. During the cold season *Synura* and *Uroglena* species (Chrysophyceae) are predominant while *Eudorina-Pandorina* and *Volvox* (Chlorophyceae) are very common during rest of the year. In these shallow habitats it is difficult to separate planktic and attached algae. In the latter group there is a high number of desmid species that thrive in the soft, often humic waters, and there is a good number of diatoms as well. The total number of algal species cannot be estimated but must be in the order of several hundred.

Higher Plants

The Zambesian Phytochoria is one of 16 areas in Africa defined as having more than 50% endemic plant species and more than 1,000 such species in total.

Species number. We owe the best floristic information on the Okavango Delta to the late Peter A. Smith (†1999) who already began the study of the Okavango flora in the early sixties. Although his unexpected death impeded the publishing of his enormous knowledge, some fragmental work remained and it forms the foundation for the current floristic research.

Smith compiled the first plant species list (vascular plants) for the Okavango Delta within the scope of the Ecological Zoning of Okavango Delta (SMEC, 1989) using the analysis of records of authenticated plant specimens from herbaria containing a major collection of Botswanan material (Gaborone, Harare, Kew-London, Pretoria) supplemented by references in the botanical literature and his own records. This list contains 1,061 different species (and with lower taxa 1,078). However, Smith guessed that the final total species number might eventually approach about 1,200 at least, since many remoter parts of the Delta had still to be explored botanically.

Between 2000 and 2002 several botanical studies were conducted which lead to an extended list of 1,299 species and subspecies (Ellery and Tacheba, 2003). Based on the mark-recapture method these authors estimated that the total number of species and lower rank taxa in the Okavango Delta is 1,405. However, most botanical studies have been done in the central 2/3 of the total area, while the in-accessible eastern parts in particular have hardly been studied. The total number of species is therefore likely to be considerably higher than that estimated by Ellery and Tacheba (2003).

Species diversity. The best overview of the overall floristic diversity is provided by Ellery and Tacheba, (2003), and the following paragraphs reflect their calculations. As stated before, the currently known flora of the Okavango Delta comprises about 1,300 taxa on the species and lower levels, of which 1,260 taxa are on the species level. They belong to 530 genera and 134 families. The most diverse families are the grasses Poaceae, sedges Cyperaceae, followed by the Asteraceae and Fabaceae, each of which have more than 20 genera and 50 taxa of species and lower ranks. Most genera (73%) are represented by one or two species only, whereas a small number of genera (7%) are represented by 10 or more taxa of species and lower ranks.

The life-form spectrum is clearly dominated by herbaceous plant species (hemicryptophytes 55.5%, cryptophytes 4.4%, therophytes 7.6% and aquatic plants 8.1%). Woody plants make up 18.1% of the flora, split approximately evenly between shrubs and trees, the chamaephytes contributing 6.3%. The proportion of the hydrophytes seems to be underestimated (see below).

Of the total number of taxa present in the Okavango Delta, a significant proportion of about 60% occur in dryland settings on islands or sandveld tongues. However, despite their terrestrial character many of these taxa are absent in the surrounding savanna habitats as they require a different air humidity or soil moisture regime or higher ground water table. Thus they are intimately associated with the wetland environments of the Okavango Delta (Ellery and Tacheba, 2003).

A large number of species occur in the permanent swamps (about 220 taxa), and many are connected to the flooded grasslands (about 90 taxa) or to the combination of flooded grasslands and dryland settings (80 taxa). A small number of species are parasitic (18) or insectivorous (12).

It is difficult to extract the number of aquatic and semi-aquatic (palustric) species from the species pool mentioned above. The reason lies in the ambiguous definitions of hydrophytes (aquatic macrophytes) and wetland plant species as discussed by Junk in this volume. If one follows the definition of Reed (1988) for hydrophytes, which " ... demonstrate the ability to achieve maturity and reproduction in an environment where all or portions of the soil within the root zone become, periodically or continuously, saturated or inundated during the growing season", the majority of species of the frequently inundated floodplains of the Okavango Delta belong to this category. Smith (SMEC, 1989) with his extensive experience of the Delta flora classified it as outlined below (Table 2).

Of the 147 plants classified as aquatic and semi-aquatic only 10 are woody of which only three are trees. The palm *Phoenix reclinata* and *Syzygium guineense* are fully grown trees that occur in patches fringing islands or termitaria, while the shrubby *Ficus verruculosa* lines the lower reaches of river channels in the perennial swamp (op. cit.).

The "conventional" aquatic plants such as submersed species or species with floating leaves develop such large morphological plasticity in the floodplains that the affiliation to a certain class is dependent on the environmental conditions at the time of the investigation. For example *Nymphoides indica,* a hydrophyte with floating leaves in permanent waters or during flood conditions, is able to develop a terrestrial form with compact leave rosettes as soon as the floodplain dries up and thus resemble terrestrial geophytes. There are, therefore, unavoidable overlaps in both life form classification and in habitat grouping, which reflects the fact that large variations in flooding (see above) cause the selection of plants with large ecological, physiological and morphological plasticity. From Smith's data (SMEC, 1989) it can be estimated that 35% of all species occur in more than one habitat along the dry – wet gradient (Table 3).

Species/area relationships. Ellery and Tacheba (2003) list 1,259 species for the Okavango Delta for an area of

Table 2. Analysis of Okavango Delta plant species by lifeform (After Smith in SMEC, 1989).

	Total	Dicots	Monocots	Ferns
AQUATIC & SEMI-AQUATIC PLANTS				
Emergent grasses & sedges	61		61	
Other emergent herbs	76	55	19	2
Trees & shrubs	10	9	1	
Subtotal	**147**	**64**	**81**	**2**
Submerged sedges	2		2	
Submerged other herbs	19	5	14	
Subtotal	**21**	**5**	**16**	
Emergent and submerged herbs and creepers	11	10		1
Free floating on surface or submerged	16	7	7	2
Floating leaved	13	9	4	
Subtotal	40	26	11	3
TOTAL AQUATIC PLANTS	**208**	**95**	**108**	**5**
NON-AQUATIC PLANTS				
Forbs	383	328	50	5
Grasses	168		168	
Sedges	60		60	
Creepers	78	77	1	
Subtotal herbs	**689**	**405**	**279**	**5**
Woody shrubs & shrublets	85	84	1	
Shrubs or trees	28	28		
Climbers	8	8		
Trees	60	59	1	
Subtotal woody plants	**181**	**179**	**2**	
TOTAL NON-AQUATIC PLANTS	**870**	**584**	**281**	**5**
GRAND TOTAL	**1,078**	**679**	**389**	**10**

25,000 km^2. Since the ratio species (S)/area (A) is not linear, but typically follows a function: $c = S : A^{0.18}$ (Rosenzweig, 1995), comparisons of species richness between areas of different size must take this into account. In the formula above c is the number of species expected to be found in an area of one km^2. This value calculated for a number of biomes in Southern Africa (Table 4) shows that the Okavango Delta has a species density of 210 species per km^2 similar to the dry Karoo biomes in South Africa. This is corroborated further by inserting the Okavango data in a log/log diagram with 25 biomes from South Africa outside of the extremely species rich Cape Floral Kingdom (Rosenzweig, 1995). The Okavango data falls almost exactly on the regression line reflecting similarity to the dryer and colder southern and western biomes, while the species densities are more than twice as high for the better watered and warmer grasslands and savannas in the eastern and northern parts of the sub-continent (Table 4).

Plant communities, their dynamics and species richness. Several vegetation studies have been done in the Delta on the plant community level within the last two decades (SMEC, 1989; Ellery et al., 1993; Ellery et al., 2000; Bonyongo et al., 2000; Ellery and Tacheba, 2003; Hermann, 2003; Sliva et al., 2004), which have resulted in various suggestions concerning vegetation classification. Most of these have been restricted to limited objectives,

Table 3. Number of plant species observed in each habitat (after Smith in SMEC, 1989, simplified). Note that some species occur in more than one habitat.

Habitats	Number of observed species
Perennial swamp	205
Seasonal swamp	240
Flooded grasslands	213
Drylands	686
Miscellaneous	84
Total	**1,428**

but regardless if the methods employed were quantitative and statistical or based on more qualitative assessments, the over riding result is always the same. The major factor organizing plant communities in the Delta is the hydrology and more specifically the duration and depth of flooding.

A classification of plant communities was done based on quantitative data covering a fair amount of Delta habitats (Sliva et al., 2004), producing a dendrogram using TWINSPAN (Fig. 6). This clearly shows that on each level of division the hydrological conditions are decisive.

At the first level of division the samples were split into group 2, which represents the wet (inundated or frequently flooded) wing of the community spectrum, whereas group 3 represents seasonal floodplain and island communities. In the next step, water depth and flood duration are responsible for the division: group 4 is characterised

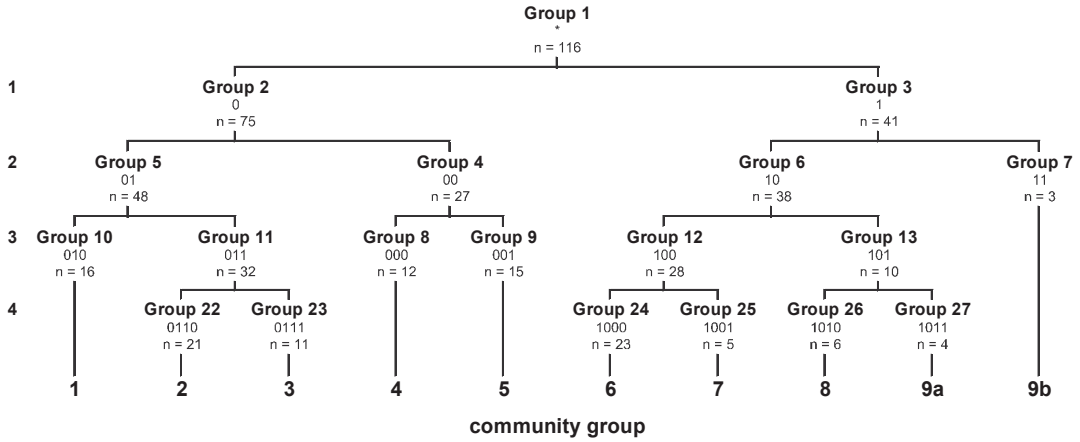

Figure 6. Dendrogram showing the TWINSPAN hierarchical division of samples into plant communities. See text for the description of the community groups.

Table 4. Number of plant species per 1 km^2 area in the Okavango Delta and other Southern African biomes. Data compiled from Smith in SMEC (1989) and Ellery and Tacheba (2003).

Biome	No. species	Area (km^2)	Species per 1 km^2 (4)
Savanna	5,788	632,034	523
Desert	497	41,292	73
Grassland	3,788	111,888	467
Fynbos (1)	7,316	36,628	1,104
Nama-Karoo (2)	2,147	198,468	239
Succulent Karoo (3)	2,125	50,516	302
Okavango (Ellery)	1,259	25,000	210

(1) The maccia like vegetation which is dominant in the Floral Kingdom Capensis and covers the southern most part of Africa.
(2) Karoo: The semi-desert Floral Domain located north of Capensis and south and west of the Zambezian Floral Domain and the Kalahari. It stretches along the western part of southern Africa up to Angola and is divided into a number of sub-domains of which Nama Karoo Sub-domain is bordering the Kalahari.
(3) The Succulent Karoo sub-domain is located in the mountainous area of western Cape Province and is characterized by many succulent plant species (see Werger and Coetzee, 1978).
(4) The species per 1 km^2 (c) is a measurement of species density based on the formula: c = Species number : Area $^{0.18}$ (km^2) (Rosenzwieg 1995). This is the expected number of species in one square kilometre.

by the indicators *Schoenoplectus corymbosus* and *Miscanthus junceus* (frequently inundated floodplains), whereas group 5 is indicated by the presence of *Vossia cuspidata*, *Ceratophyllum demersum* and *Cyperus papyrus* (open water and permanent swamps). The broad spectrum of seasonal swamp and island communities is contained in group 6, which is specified further on the next level of division, while group 7 contains a special pan vegetation. After the fourth level of division nine meaningful ecological vegetation groups were identified: (1) Vegetation of open water, (2) *Cyperus*-dominated channel fringe and backswamp communities, (3) *Phragmites*-dominated channel fringe and backswamp communities, (4) *Miscanthus-Ficus* permanently flooded backswamp communities, (5) *Schoenoplectus corymbosus-Cyperus articulatus* communities of shallow backswamps and frequently inundated floodplains, (6) Communities of seasonal floodplains, (7) Island fringe communities, (8) Island interior grassland communities, (9a) Pan communities – upper level, (9b) Pan communities – bottom level.

In the DCA ordination graph (Fig. 7), these nine major communities identified by the TWINSPAN arrange neatly along axis 1 which can be explained by the depth and duration of flooding. Axis 2 is also predominantely related to hydrology, but here the main gradient is upstream-downstream with low annual water level variations in the upper parts of the Delta (0.5 m) and much higher variations in the lower parts (2 m). The third major environmental factor is hydrological as well; the difference between lentic and lotic habitats.

Recognising the different seasons, scale and focus of all the different vegetation studies and considering our own latest data (unpubl.), about 26 meaningful ecological plant communities can be preliminarily classified in the vegetation of permanent swamps, floodplains and islands. The drylands remain unconsidered, which are the never flooded vegetation of large sandveld tongues and large islands representing the Acacia and Mopane woodlands and shrubland, as well as the non-inundated grassland types (Table 5).

Communities associated with permanent water (No. 1–14) are relatively species poor, harbouring about 50 to 70 species per community group. *Cyperus papyrus* as well as *Phragmites* species tend to develop large and dense monospecific stands, supported by the relatively higher nutrient loadings in the upper reaches of the Delta, making the establishment of other less competitive species difficult. The species diversity increases on the open boundaries, thus along the channel and lake fringes. In open water areas (ledibas, oxbow lakes) the diversity rais-

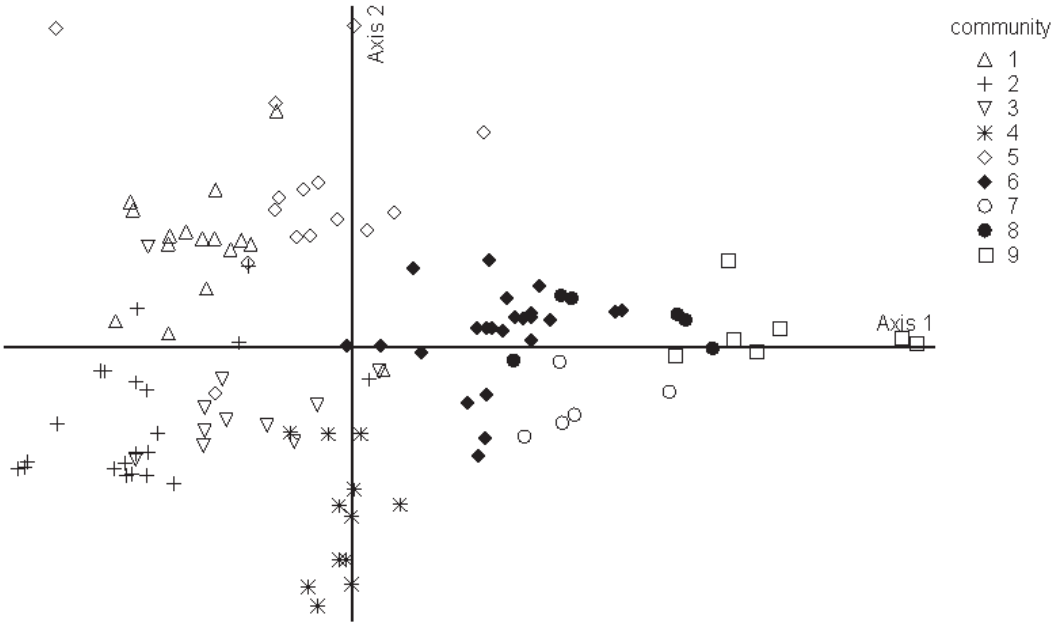

Figure 7. DCA ordination graph of the 116 vegetation samples (Sliva et al., 2004). For names of communities see Table 5.

es with the shallowness of the water. The species composition and abundance in these communities remains similar through the whole year independent of the flood pulse (Czekanowski index of similarity 0.70–0.95).

Compared with permanent aquatic communities, the number of plant species rises up to twofold on seasonal floodplains (No. 15–20). On regularly inundated floodplains the water fluctuation causes periodical changes between terrestrial and aquatic phases of the sites. The aquatic-terrestrial-transition-zone, "ATTZ" (Junk, 2003) is a dynamic system of steadily changing water and nutrient status, of establishment and dying off of species. This dynamic littoral zone provides good living conditions for both terrestrial and semi-terrestrial short-lived plant species during the low water period as well as for aquatic species during the inundation, as long as these species are able to survive the unfavourable period or to colonise and occupy the new habitats rapidly enough. The availability of various temporary habitats which are densely packed within relatively small areas is responsible for the high species diversity. If one compares the low and high water season, the alteration of species and their abundances within the floodplain communities is also expressed by the significantly lower similarity indices (Czekanowski) of 0.25–0.50.

However, the highest species diversity is exhibited in the riparian woodlands along the island margins (No. 21–22). During the field campaign in February 2003 between 20 and 83 species were recorded per 70 m^2 plot, and altogether more than 150 species (e.g. more than one eighth of the whole Okavango flora) were identified within only five plots (Sliva et al., 2004). Island margins provide optimal habitat for a large number of woody species (shrubs and trees), which increase the species diversity considerably. After exclusion of woody species the (Czekanowski) similarity index of vegetation recorded during dry and rainy season is only 0.22–0.25, which reflects the distinctive seasonal variation.

The origin and the unique ecological functions of islands and associated woodlands has been subject of several in-depth studies (McCarthy et al., 1991; McCarthy et al., 1993; Ellery et al., 1993; Ellery and Tacheba, 2003). In this environment the classification of the riparian plants as dry land species is ambiguous as the riparian zones are fed by shallow horizontal groundwater infiltration from adjacent rivers and floodplains (Ramberg et al., 2006). The majority of woody species (trees, shrubs and lianas) which occur within these riparian bands in the island fringes of the Okavango Delta are probably able to tap this groundwater resource (Ringrose, 2003). Even though these are not strictly wetland habitats, they are central for the present structure and functioning of the whole ecosystem (Ellery and Ellery, 1996; Ellery and Tacheba, 2003), and the fact that we find the highest species diversity in these island fringe communities underpins their high ecological value.

Next to the hydrological factor complex, the salinity of the island soils influences the diversity of species within small areas. There is a gradient of increasing solute concentration in the ground water from the edge of the islands towards the centre (McCarthy et al., 1991; Ellery et al.; 1993) which is reflected by a typical zonation of

Table 5. Overview of main vegetation groups in the Okavango Delta (except dryland habitats). Twinspan: The numbers correspond with the Twinspan classification (Fig. 6).

Open water communities:		**Twinspan (Fig. 6)**
Communities of lakes and standing backwater		
1	Nymphaea nouchalii communities	1
2	Eleocharis dulcis communities	1
3	Ceratophyllum/Lagarosiphon/Ottelia communities	1
4	Trapa natans communities	1,2
5	Vossia/Echinochloa pyramidalis communities	1,2
Communities of floating waters (channel beds)		
6	Nesaea/Potamogeton communities	1,5
Channel/lake fringe and backswamp communities:		
7	Trapa natans communities	2,1
8	Vossia/Echinochloa pyramidalis communities	2,1
9	Scirpus cubensis/Pycreus mundii communities	2
10	Fimbrystilis dichotoma/Pycreus flavescens communities	2
11	Cyperus papyrus fringe and backswamp communities	2
12	Phragmites australis/P. mauritianus fringe communities	3
13	Miscanthus/Ficus verruculosa backswamp communities	4
14	Ficus verruculosa/Syzigium cordatum fringe communities	–
Communities of frequently flooded seasonal floodplains:		
15	Schoenoplectus corymbosus/Cyperus articulatus communities	5
Communities of the Aquatic-Terrestrial Transition Zone ATTZ (*sensu* Junk)		
16	Panicum repens grassland communities	6
17	Cynodon dactylon/Sida cordifolia communities	6
18	Imperata cylindrica/Setaria sphacelata grassland communities	6
Communities of rarely flooded floodplains		
19	Urochloa mossambicense/Pechuel-loeschea leubnitzae communities	–
20	Acacia/Colophospermum shrubland communities	–
Island communities		
Riparian woodland communities		
21	Phoenix reclinata/Ficus sycomorus woodland communities	7
22	Hyphaene/Diospyros mespiliformis woodland communities	7
Island interior communities		
23	Eragrostis sp./Acacia sp. grassland communities	8
24	Sporobolus spicatus grassland communities	8
25	Urochloa trichopus/Glinus bainesii/Litogyne pan communities	9a
26	Eragrostis pilosa/Lemna pan communities	9b

vegetation and the establishment of characteristic communities (No. 23–24). On sites with high solute concentrations species diversity declines considerably since only few species are adapted to those harsh living conditions. Although the communities of saline soils seem to be the species poorest among all other communities in the Okavango Delta (with only about 20 species), they contribute to the overall species diversity because of the occurrence of the specialised halophytes.

Small ephemeral water bodies (pans) occur during the rainy season in drier habitats and carry the next specific plant communities (No. 25–26) with a distinct zonation according to the water depth and duration.

It is obvious that the main reason for the high plant species diversity of the Okavango Delta as well as for the exceptionality of this ecosystem from a nature conservation point of view, lies in the interaction of periodical natural phenomena – the annual flood in the dry season and the distinct rainy season in time of low water level – with the shifts in flooding pattern over short and long periods. Succession processes at different phases of development are therefore ongoing in all plant communities in the Delta. These processes are the main driving forces for the species and habitat diversities in the Okavango Delta and must be conserved in order to maintain the uniqueness of this system.

Invertebrates

The data on invertebrate species in the Okavango Delta is far from comprehensive and many taxonomic groups are too difficult to collect, or nobody has tried to sample them, while some are taxonomically not well known or there are no taxonomists able to identify them. The picture will, therefore, be patchy and will probably remain so for a long time.

Table 6. Overview of Odonata families, number of genera and species found in the Okavango Delta.

	Genera	**Species**
ZYGOPTERA		
Calopterygidae	1	1
Lestidae	1	5
Coenagrionidae	6	25
Platycnemididae	1	1
Protoneuridae	1	1
Subtotal	**10**	**33**
ANISOPTERA		
Aeshnidae	1	4
Gomphidae	4	7
Cordulidae	2	5
Libellulidae	22	45
Subtotal	**29**	**61**
Grand total	**39**	**94**

Dragonflies (Odonata). Comparatively good information exists for Odonata (Pinhey, 1967; 1976). Pinhey collected samples in the Okavango area during a number of expeditions until 1976 and also obtained access to other smaller collections. During 2000–2002 a new study was conducted (Kipping, 2003) which was designed to cover the same areas and habitats as those of Pinhey. A total of 94 species were found, 33 Damselflies (Zygoptera) and 61 Dragonflies (Anisoptera) in the Okavango Delta (Table 6) out of 114 species in all of Botswana.

Comparisons with species inventories from the countries surrounding Botswana (Zimbabwe, Namibia, Zambia, RSA, Mocambique) resulted in a total number of 295 species for this area. Cluster analysis revealed that there are strong similarities in Odonata composition in particular with Zambia and Namibia (the Caprivi strip); in other words with the wetlands to the north, which at wetter times have been directly connected to the Okavango. Many of the Odonata in the Delta have a Central African distribution and reach their southern most distribution here (Kipping, 2003).

Pinhey (op. cit.) recorded a total of 92 species in the Delta. Twenty-five years later Kipping (op. cit.) found one species new for the area and one new for science. On the other hand he could only find 70 out of the 92 species found by Pinhey, although his sampling intensity compares well with that of Pinhey both in time and space. Nine of the "missing" species are Zygopterans and seven of them had been recorded from three or more localities in the Delta. Out of the 13 Anisopterans that could not be found again, five had been found in three or more localities. For the species found in only 1–2 localities the problems of sampling rare species arise. However, when there are indications that species which were fairly wide spread up to the mid-seventies are now absent, there are reasons to look for other explanations. There has been a gradual decline in flooding of the Delta since the mid-seventies which could have resulted in a loss of suitable aquatic habitats for the larvae or in a loss of suitable flying prey for hunting adults. Another factor is the aerial spraying against tsetse flies in the Delta which took place during the eighties and then again 2001–02. During the first period fairly potent insecticides such as dieldrin were used but over smaller areas in each year. In the recent spraying, however, the entire Delta south of the Panhandle was sprayed; the northern part in 2001 and the southern part in 2002; totaling to about 17,000 km^2. Deltamethrin was used which has some good properties such as its short half-life in nature and its specificity for invertebrates. Adult Odonata experienced high mortality during the spraying of deltamethrine and the same results were recorded for larvae of the families living on the sediment surface or on vegetation (Ramberg, 2004).

Butterflies (Lepidoptera). A preliminary checklist of butterflies of Botswana, including the Okavango Delta, was published by Pinhey (1968; 1971; 1974; 1976). This checklist is based on his own collecting expeditions, supplemented by records from museums in Southern Africa. Pinhey's coverage of the Okavango Delta is limited mainly to the southern and western Okavango from Maun to Mohembo, due to the inaccessibility of the Delta at the time. Nevertheless, 115 species were recorded from this area. Pinhey's work forms the baseline for butterflies in the Okavango. Very little other information has been published since 1976.

The Nymphalidae and Lycaenidae are the most diverse families in the Okavango Delta (Table 7), despite the abundance and conspicuousness of the Pierids (Pinhey, op. cit.). The vast majority of butterflies encountered in the Delta belong to this last family, and are restricted mainly to two very abundant migratory species – *Belenois aurota* (Brown-veined White) and *Catopsilia florella* (African Migrant). Large numbers of these two butterfly species migrate in a north-easterly direction throughout the region, including the Okavango, in mid-summer. The Lycaenids by contrast are small, inconspicuous species, which nevertheless contribute to over 30% of the observed diversity.

Analysis of Pinhey's Checklist of Butterflies of Botswana shows that the Okavango Delta is a focus of butterfly diversity in Botswana. This is not unexpected since this is a wetland area surrounded by arid Kalahari semi-desert – a wide variety of habitats exist with a wide range of larval food plants, and angiosperms which provide nectar for the adult butterflies. Some species such as *Danaus chrysippus* and *Vanessa cardui* are cosmopolitan, while others are characteristic of wetlands such as: *Hyalites rahira*, *Precis ceryne*, *Myrina silenus*, *Borbo micans*, *Parnara monasi* and *Gegenes hottentota*.

In the Okavango Delta, the butterflies most at risk are the myrmecophilous (ant-associated) Lycaenids. As larvae these species require both the host ant and the host plant, as well as optimal climatic conditions to thrive. Due to the paucity of information on the Delta's butterflies, no Lycaenids have yet been identified as threatened, although it is possible that some species are at risk.

Table 7. Overview of butterfly families and species in the Okavango Delta. The taxonomy follows Pringle et al. (1994).

Family	Nr. of species
Nymphalidae	36
Lycaenidae	39
Pieridae	23
Papilionidae	3
Hesperiidae	23
Total	**124**

There are no documented ENDANGERED or VULNERABLE butterfly species in the Okavango (Henning and Henning, 1989). The following species are RARE: *Anthene minima*, *Colotis doubledayi angolanus*, *Pseudonympha swanepoeli* and *Tuxentius malaena*. *Borbo micans* and *Gegenes hottentota* are placed in the INDETERMINATE category.

Mollusca. The occurrence of aquatic snails has been fairly well documented in several studies compiled by Murray (1997). These studies are combined in Table 8. Most of the aquatic snails found in the Okavango Delta are widespread in the Afrotropical region. The most southerly localities known in Africa for populations of *Pila* and *Gabbiella* (op. cit.) are found here and only one species out of 16 may have some affinity with temperate climates. There are no endemic snail species and many of them occupy seasonal waters scattered over huge areas of the African savanna. Despite the great distance, (nearly 3,000 km), between the Okavango and the Sudd in the Nile River, 9 species of their total fauna of 34 species live in both areas (op. cit.).

Zooplankton. In total 37 microcrustaceans have been recorded in the Delta by Lindholm (2006), Hart (1997), and Hart et al. (2003). There are 16 species of copepods within six genera, with *Microcyclops* and *Tropodiaptomus* being dominant and 45 cladoceran species (Lindholm, 2006). Most are minute, reflecting the strong predation pressure from visually feeding fish fry. *Moina micrura*, *Daphnia laevis* and *Simocephalus vetulus* are dominant and widespread species, especially on many floodplains (Högberg et al., 2002).

Three different zooplankton habitats may be distinguished in the Delta: permanent lakes, seasonal floodplains and isolated temporary rain pools. Among these, seasonal floodplains offer the most diverse zooplankton fauna. During high water periods, the production of ostracods, copepods and cladocerans can be extremely high temporarily. Nearly 90 g DW L^{-1} zooplankton biomass has been recorded, making zooplankton on seasonal floodplains a crucial link in the aquatic food web (Högberg et al., 2002).

Fish parasites. Jo Van As and his research team have identified no less than 200 fish parasite species in long term studies, many new to science. Most of these species have complex life cycles involving one, two or three specific hosts such as trematode – snail – fish – bird. Such relationships can probably only evolve over very long evolutionary time scales and may reflect the old age of the Delta ecosystems as a functioning whole, even if the evolutionary processes have taken place elsewhere. Since this field is under-researched in tropical and subtropical areas, no meaningful comparisons can be made (Van As, pers. com.).

Table 8. Overview of number of aquatic Mollusca species found in the Okavango Delta.

	Genera	**Species**
Gastropoda (snails)	13	16
Bivalvia (mussels)	4	6
Total	**17**	**22**

Effects of aerial spraying against tsetse flies. The aerial spraying of the entire Delta (except the Panhandle) against tsetse flies 2001 and 2002 using deltamethrin (0.26–0.30 g/ha) was repeated five times during the cold season May–August. A large number of samples were collected for the environmental assessment of both aquatic and terrestrial environments (Perkins and Ramberg, 2004a). This study has, however, several weaknesses which makes it less useful in the present context. No benchmark studies were conducted before the spraying began and taxonomic identification was only taken to the family or genus level. For some taxonomic groups (usually the most common) the identification went a step further and species were identified as such but not given a species name only an identification number, so called "morphospecies".

After spraying, aquatic invertebrate families showed a 25–46% reduced total abundance (Palmer, 2004). Before spraying there were statistically significant differences in species compositions between lagoons and streams, but due to the disappearance of several families after the spraying, these differences became less apparent and a species poorer, less diverse composition remained. Out of a total 65 taxa 23 were common, and of these, six taxa with several species in each, declined drastically during the spraying campaign and had disappeared by the fifth spraying cycle. It is likely that at least the same proportion of the less common taxa was eliminated as well.

Terrestrial invertebrates were predominantly sampled from under tree canopies (as knockdown) before, during and after the five spraying cycles (Dangerfield, 2004). Abundances declined by up to 68%. The most affected group was beetles. The composition of species changed through the cycles. Around 30% of the species were only collected before the spraying or in the first spraying cycle, whilst a lower proportion appeared in later cycles for the first time.

The recovery of the invertebrates was studied during 2003 at the same sites as in the previous year. Some of the aquatic families affected by spraying remained at reduced levels, notably shrimps and small backswimmers. Many of the affected families returned to pre-spraying abundances and the composition of aquatic invertebrates in the sampled habitats returned approximately to their pre-spraying patterns (Palmer, 2004).

Abundance of terrestrial invertebrates returned to pre-spraying levels within one year. However, about 30% of the species found before or in the beginning of the spraying in 2002 could not be found again in 2003. On the other hand about the same number of new species occurred for the first time in this later year (Dangerfield, 2004). It is not known how much of this reflects a natural pattern and how much is a result of rare species taking over niches that became empty due to extermination; in particular as most of these changes occurred among the rare species (Ramberg, 2004).

Fish

The Okavango system has been connected to the Upper Zambezi drainage basin and its fish fauna can be considered as being part of the Zambezi system, which has some 134 species of fish (Skelton, 2001). Of these 86 are found in the Okavango basin and 71 within the Okavango River and Delta below the Popa Rapids of the East Caprivi Strip in Namibia (Table 9). More than 50% of the Zambezi species also occur in the Congo Basin and Lake Malawi. There are also some similarities with the fish fauna of the Limpopo and Phongolo River Systems to the south-east. This is probably the result of river capture in the not so distant past. The Zambezi fauna includes 23 (17%) endemic species, most of which are restricted to the upper Zambezi (Skelton, 2001). There are, however, no endemic species restricted to the Okavango River and Delta below the Popa Rapids. So far no alien introductions or translocated fish have been found in the Okavango River and Delta.

The most important factors influencing the distribution of fishes in the Okavango system are the permanence and the flow rate of the water. Specialist rheophilics and species adapted to rocky habitats such as the slender stonebasher *Hippopotamyrus ansorgii* (Mormyridae), the river sardine *Mesobola brevianalis* (Cyprinidae), the mountain catfish *Amphilius uranoscopus* (Amphiliidae), the broadhead catfish *Clariallabes platyprosopos* (Clariidae) and the Okavango rock catlet *Chiloglanis fasciatus* (Mochokidae) are confined to the Angolan headwaters of the Okavango River and riverine floodplains and are not found in the Delta below the Gomare fault.

Fish stock assessment. Compared with a large number of African lakes and rivers the number of fishermen per square km is extremely low in the Okavango Delta (Mosepele, 2000). Locally household fishing may be important, but large areas of the swamp are not accessible by boat due to vegetation blockages and the risk of Hippopotamus attacks. The total yield of the fishery is low, and the catch per unit effort (CPUE) very low (0.4 kg/Lundgren gillnet set) compared with ten other aquatic systems in Africa which had a range of 1.4–4.2 kg/set (op. cit.). This does indicate an overall low fish biomass in the Delta and reflects its low nutrient status. Locally, however, the seasonal floodplains have a much larger density of fish than the permanent swamp and streams (Högberg et al., 2002). Occasionally very high densities occur before and during spawning, as well as in drying-up pools that have been isolated from the streams. Here fisheating birds aggregate in large numbers.

Table 9. Fish families, number of genera and species in the Okavango system and Okavango below the Popa Rapids. Compiled from Skelton et al., 1985; Merron, 1993; Skelton, 2001; 2002 and own data (Van As) from annual collections 1997–2004.

Family	Genera (n)	Species (n) Okavango System	Species (n) Okavango below Popa Rapids
Mormyridae	5	6	6
Kneriidae	2	2	0
Cyprinidae	5	25	17
Distichodontidae	2	3	3
Characidae	4	4	4
Hepsetidae	1	1	1
Claroteidae	1	1	1
Amphiliidae	2	3	2
Schilbeidae	1	1	1
Clariidae	2	7	6
Mochokidae	2	8	6
Poeciliidae	1	3	3
Cichlidae	7	18	18
Anabantidae	2	2	2
Mastacembelidae	1	2	1
Total	**38**	**86**	**71**

Habitat selection, form and function. Morphological features such as body shape, size and shape of fins, placement of eyes and size and shape of mouth can be used to construct an ecomorphological classification of Okavango fishes. The structural similarities in unrelated species of fish can be correlated with their habitat and niche. These vary from open water, mid-water, surface and bottom dwelling species, as well as species with special adaptations to inhabit the dense vegetation in papyrus beds.

Open and midwater fast swimmers. Fishes in this category have a fusiform (tapering at both ends) body shape with forked or lunate caudal fins and large, laterally placed eyes. The dorsal and anal fin is short and acts as a rudder for maneuvering at high speed. These fish are all predators mostly in the upper layer of open water of flowing rivers usually in roving shoals. The typical example of this category is the tigerfish *Hydrocynus vittatus* (Characidae) which occurs in the Panhandle and upper part of the Delta. Other fishes in this category include some of the barbs (Cyprinidae) and other characins. Unlike the tigerfish, these are all small species.

The African pike *Hepsetus odoe* is the sole representative of its family, Hepsetidae and occurs widespread in Africa in the Upper Zambezi, Congo and Niger drainage

basins. Its body plan fits comfortably in this category, but its hunting methods differ from that of the tigerfish. It prefers the quiet waters of channels and lagoons where it stalks its prey, going for the kill in a swift rush. They do not co-exist in the same habitats as tigerfish, which prefers the fast flowing currents of the river.

Midwater slow swimmers. The body shape of fishes in this category is deep and laterally compressed. The caudal fin is truncated and deep, the dorsal fin is long and extends from directly behind the head to the base of the tail stem, the anterior part with spines and the posterior part with flexible soft rays. All the fins are broad providing these fish with excellent agility and the ability to hover in the open waters and in the vegetation of lagoons. This category includes the tilapias of the genera *Oreochromis* (2 species) and *Tilapia* (3 species) and some of the bream of the genus *Sargochromis* (2 species), all from the family Cichlidae. They all have relatively small mouths and feed on plants, insects and detritus, while some are omnivores. The Zambezi river bream *Pharyngochromis acuticeps* also falls in this category, although it prefers sheltered habitats. Other cichlids in this category are the banded jewelfish *Hemichromis elongatus* and the southern mouthbrooder *Pseudocrenilabrus philander*. The latter species has a very wide distribution in southern Africa ranging from the Orange-Vaal to the Congo systems and extending to Lake Malawi. It is, together with *Tilapia ruweti*, the smallest of all the cichlids in the Okavango system.

The agility of movement as a result of the laterally compressed body plan and broad fins paved the way for a group of species within this category to fill a niche as predators. Their thin profile facilitates stalking of small fish in the vegetation of lagoons and along the riparian vegetation. They have exceptionally large mouths, hence their common name largemouth breams. All the predator breams belong to the genus *Serranochromis* of which there are six species in the Okavango system.

Surface feeders. This category comprises the topminnows or lampeyes of the genus *Aplocheilichthys* (Poeciliidae), with three species and a possible new species present in Botswana. They occur in small shoals throughout the Okavango River and Delta and are abundant serving as a food source for many birds and other fish. Lampeyes are adapted to feed on insect larvae and plankton, very often on the surface of the water. Their abdomen is rounded but their dorsal surface is flat allowing them to feed at the surface of the water without exposing their bodies to predators from above. They have exceptionally large eyes placed near the top of their heads. This is no doubt an adaptation for locating their prey as well as avoiding predators. Another adaptation for its surface feeding lifestyle is the fact that their mouths face upward.

Bottom dwellers. The bodies of fishes in this category are dorso-ventrally compressed and their mouths face downward. Their eyes are placed on the dorsal side of the head. These are the only features, which the bottom dwellers have in common since the benthic habitat does not present a uniform niche. Benthic dwelling fish occupy a variety of trophic levels. Their food sources range from detritus, benthic algae, and a wide range of adult and larval insects, oligochetes, snails or even other fishes.

The catfishes (Clariidae) are represented by six species in the Okavango system, of which the broadhead catfish *Clariallabes platyprosopos* is restricted to rocky habitats in Namibia and Angola. Catfishes are all well adapted benthic species and opportunistic omnivores that will feed on almost any available food source. They have a dominant ecological presence and at least the sharptooth catfish, *Clarias gariepinus*, can be regarded as a keystone species.

Other benthic species in the Okavango system include representatives of the family Mochokidae. The Okavango rock catlet or mouthsucker, *Chiloglanis fasciatus*, is adapted to attach to rocks and plants by its mouth, which forms a very effective sucker. Six species of squeakers of the genus *Synodontis* co-exist in the Okavango system, each adapted to fill a different niche, displaying a textbook example of adaptive radiation. The spotted squeaker, *Synodontis nigromaculatus*, feeds on detritus and hosts hundreds of individuals of five different nematodes and a whole range of ciliophorans in its rectum, probably symbionts assisting in digestion (Moravec and Van As, 2004).

Although the body plan of the squeakers is ideally suited for feeding in the benthal, it allows for a peculiar type of upside down feeding as well. We have personally observed large numbers of spotted squeakers swimming upside down on the surface of the river feasting on termites which appeared in mass after a thunderstorm. This feeding activity happened in the late afternoon and continued for a considerable time.

Another very specialized group of benthic dwellers is the sand catlets of the genus *Leptoglanis* (Amphiliidae). These small fish of no more than 40 mm bury themselves in the sand with only their eyes protruding. They are normally found in submerged sandbanks behind little patches of vegetation facing upstream in the main river and large channels. Here they prey on small planktonic creatures.

According to Skelton (2001) the taxonomy is in disarray and the spotted sand catlet *Leptoglanis rotundiceps* from the Okavango and Zambezi systems may represent a complex of several different species.

Dense vegetation and rocky habitats. Papyrus beds comprise a multitude of co-existing plant species representing a unique habitat for aquatic animals. Fish living in this submerged jungle require specific adaptations in order to find food and avoid predators in a world of almost perpetual darkness. The evolutionary road to sur-

vival in this habitat may be varied resulting in morphologically different models co-existing amongst the dense foliage within the papyrus beds.

One very successful inhabitant of dense vegetation is the spiny eel *Aethiomastacembelus frenatus*. This small eel is slender, snake-like, has a very flexible body, is very tough and fast. They occur in abundance in papyrus beds, but are so cryptic that fishermen spending a lifetime fishing the Panhandle have never encountered one. The only way of finding live specimens of these ellusive spiny eels is to physically lift a section of papyrus onto a boat and search through the root mass. The same adaptation for surviving in a papyrus root bed is advantageous when surviving in crevices and rocky habitats as the second species the ocellated spiny eel *Aethiomastacembelus vanderwaali* does successfully in upper reaches of the Okavango River.

The endemic African fish family, Mormyridae, is represented by six species belonging to five genera, all superbly adapted for life in dense vegetation in the Okavango River and Delta: The Zambezi parrotfish *Cyphomyrus discorhynchus*, the bulldog *Marcusenius macrolepidotus,* the western bottlenose *Mormyrus lacerda*, the northern churchill *Petrocephalus catostoma*, the southern churchill *P. wesselsi* and the dwarf stonebasher *Pollimyrus castelnaui*. One species, the slender stonebasher *Hippopotamyrus ansorgii*, is adapted for life in rocky habitats of the upper Zambezi and not found in the Delta.

These unusual fishes are laterally compressed with a large anal fin. The caudal fin is forked and the tail stem is pronounced. They have soft mouths adapted for taking invertebrates from plants. Their adaptive advantage for survival in dense vegetation is that they discharge a weak electrical current from an organ situated in the tail. Each species has its own distinct signature discharge and this serves as a means of communication, navigation and prey detection.

Strategies to cope with low oxygen levels. The oxygen levels throughout the River and Delta below the Popa Rapids are generally low. Even in the fast flowing main stream saturation levels are between 50–70%. In seasonal floodplains and back waters oxygen levels rarely exceed 3 mg/L, and at night often drop below 1 mg/L which is close to lethal for many fish species.

Despite the low oxygen level, the floodplains have other advantages making it a suitable habitat for many fish species. It has a high productivity and provides a relatively sheltered environment against predators, therefore many fish species occur there and have adapted to the low oxygenated environment.

All five representatives of the catfish family, Clariidae, found in the Okavango have accessory air-breathing organs in their gill chambers, and the two climbing perch species have accessory air-breathing organs in chambers above the gills. Many of the cichlid species have physiological adaptations to survive low oxygen levels, but for a significant number of species the strategies of overcoming the fundamental problem of low oxygen levels are still unknown.

Low oxygen levels could be lethal for eggs and larvae. To deal with this problem, all cichlid species have special strategies to provide a better-oxygenated environment for eggs and fry either by mouth brooding or by fanning and guarding eggs laid in nests (Skelton, 2001).

The African pike and the climbing perches build nests of bubble foam on the water surface under which spawning takes place. The eggs float and are then trapped in the foam where oxygen levels are high. These floating nests are vulnerable to predation and are guarded by the males. In some fish species, such as catfish, the eggs are sticky and attach to vegetation, which will keep them away from the frequently anoxic sediments. At least 19 species representing 24% of the Okavango fish fauna have evolved strategies to care for eggs and fry.

Endemic species. The fish fauna of the Okavango River and Delta are now, for all practical purposes, isolated. The link between the eastern part of the Delta and the Zambezi, the Magwegqana River, also called the Selinda spillway, no longer receives water. However, this river was flowing to the Zambezi even in the recent past during wetter periods and there are no endemic fish species in the Okavango. The physical conditions in the Delta especially in floodplains, can however be extreme in terms of low oxygen levels at night and low temperatures during the winter. These conditions could result in considerable evolutionary pressure for those species surviving here, but the time for speciation, since the last drying up of the Delta, has probably been to short for new species to evolve.

Reptiles and amphibians

In total 33 amphibians and 64 reptiles have been recorded in the Okavango Delta (Murray, 1997).

All amphibians are dependent on water at least for reproduction and/or deposition and hatching of the eggs. Most of the 33 amphibian species occur close to water and only 3–5 species are more terrestrial. The most pronounced of these is *Chiromantis xerampelina,* which spends the entire life in trees – even during reproduction. The eggs are deposited in a bubble nest above temporary water pools when they are still dry. When the rains come the eggs are washed down into the water. On the other hand only two amphibian species (*Xenopus laevis* and *X. muelleri*) are fully aquatic. Most other species select habitats close to water and some have adopted strategies of hibernation or aestivation to survive temporal and seasonal desiccation of habitats.

Out of the 33 species in Botswana (Table 10) twelve (36%) have a distribution restricted to the Okavango and

the Chobe and eight (24%) are confined to the Okavango Delta only. These species are tropical and the Okavango Delta is commonly the southern end of their distribution.

Out of 64 reptile species (Table 11) recorded from the Delta the four terrapins (Pelomedusidae), *Varanus niloticus*, the Nile Crocodile and one snake (*Crotaphopeltis barotseensis*) are confined to water, while the python and four snake species in Colubridae mainly occur in swamp habitats. Most reptiles, 52 in all, are thus terrestrial. Most of these have a wide distribution in southern and central Africa. There are on the other hand 10 species whose distribution in Botswana is restricted to the Okavango and the Chobe. Seven of them are aquatic or swamp species and have a northern-tropical distribution. Two species are terrapins and the other five are snakes.

Birds

The number and variety of birds in the Okavango Delta is well documented, due largely to the efforts of amateur birdwatchers who contributed substantial data to the Bird Atlas of Botswana between 1980 and 1990. This database, where birds have been recorded in a standardized way for the whole country, has subsequently been kept updated by the Records Sub-committee of Bird Life Botswana. The analysis of bird diversity that follows is drawn from these sources, supplemented by personal observations (Table 12).

There are 444 confirmed bird species occurring in the Okavango Delta. This makes the Delta together with the Chobe River, the most species-rich area in Botswana. Most are widely distributed species belonging to 74 families of which the most important in terms of number of species are the following:

Accipitridae (eagles, hawks, buzzards, kites): 38 species. This family includes the African Fish Eagle *Haliaeetus vocifer* and African Marsh Harrier *Circus ranivorus* as two typical wetland species.

Sylviidae (warblers, apalises, cisticolas *etc*.): 31 species. One of the warblers (Greater Swamp-Warbler *A. rufescens*) and three cisticolas (Red-faced Cisticola *C. erythrops*, Luapula Cisticola *C. galactotes*, Chirping Cisticola *C. pipiens*) are wetland species with their ranges in Botswana largely confined to the Okavango Delta.

Ploceidae (sparrows, weavers, bishops, widows, queleas): 25 species. Eight members of this family are wetland species, with substantial populations in the Okavango Delta, as follows: Thick-billed Weaver *Amblyospiza albifrons*, Spectacled Weaver *Ploceus ocularis*, Village Weaver *P. cucullatus*, Golden Weaver *P. xanthops*, Southern Brown-throated Weaver *P. xanthopterus*, Southern Red Bishop *Euplectes orix*, Yellow-crowned Bishop *E. afer*, and Fan-tailed Widowbird *E. axillaris.*

Ardeidae (herons, egrets, bitterns): 18 species. All of the ardeids are primarily wetland species, with the exception of the Black-headed Heron *Ardea melanocephala* and Cattle Egret *Bubulcus ibis* which are widely distributed throughout Botswana (although both breed extensively in the Okavango Delta).

The Slaty Egret *Egretta vinaceigula* is the Okavango's only near-endemic bird species. It has the Okavango Delta as the centre of its distribution, and it is estimated that 85% of the global population of this species occurs here.

All members of the Anatidae are strictly wetland dependent in Botswana, and 12 species are found in the Okavango Delta. Only four of the nine kingfishers found in the Okavango Delta are strictly aquatic and piscivorous – the remainder are woodland, insectivorous species.

Table 10. Amphibian families in the Okavango Delta, number of genera and species.

Family	Genera	Species
Pipidae	1	2
Bufonidae	1	5
Microhylidae	2	3
Ranidae	6	15
Hemisotidae	1	2
Rhacophoridae	1	1
Hyperoliidae	3	5
Total	**15**	**33**

Table 11. Reptile families in the Okavango Delta, number of genera, species and wetland/aquatic species.

Family	Genera	Species	Swamp/Aquatic
Testudinidae	3	3	
Pelomedusidae	2	4	4
Gekkonidae	5	8	
Agamidae	1	3	
Chamaeleonidae	1	1	
Scincidae	5	10	
Lacertidae	3	5	
Gerrhosauridae	1	2	
Varanidae	1	2	1
Typhlopidae	1	2	
Leptotyphlopidae	1	1	
Boidae	1	1	1
Colubridae	22	31	5
Elapidae	4	6	
Viperidae	2	2	
Amphisbaenidae	3	5	
Crocodylidae	1	1	1
Total	**57**	**64**	**12**

Table 12. Taxonomic composition of confirmed bird species in the Okavango Delta.

Major groups	Families	Species
Non-passerines	33	186
Near passerines	18	79
Passerines	23	179
TOTAL	**74**	**444**

Geographic and habitat distribution. The Okavango Delta falls within the Afrotropical region. However, all around the Delta to the west, east and south there is an abrupt change from tropical vegetation to Kalahari woodland or dry savannah. Consequently, the distributions of many bird species, particularly waterbirds, closely mirror the extent of the Okavango. Nevertheless, it is not easy to classify the avifauna of the Okavango into wetland-restricted species and those that are not restricted to the wetland. For the purpose of comparison, the following three categories may be defined:

1. Aquatic species (112 spp.) – those that feed by diving, swimming or wading, or feed on shores or mudflats in the vicinity of water. These are all non-passerines with the exception of the coucals and some of the kingfishers, which are near-passerines.
2. Non-aquatic species (57 spp.) inhabiting wetland habitats such as floodplain forests, palm swamps, marshes and reed beds. The majority of these are passerines.
3. Terrestrial species not restricted to wetlands (275 spp.). These are mostly near-passerines and passerines, and members of the family Accipitridae (non-passerines).

Conservation status. Tyler and Bishop (1998) list six globally threatened and near-threatened bird species which occur in the Okavango Delta. They are shown in Table 13, updated to include two additional species listed in 'Threatened Birds of the World' (BirdLife International, 2000).

An estimated 85% of the global Slaty Egret population is restricted to the Okavango Delta. The Delta is also very important for the Wattled Crane – it currently supports the largest, single population of this species and over 15% of the global population (Beilfuss et al., 2002). The other globally threatened species are occasional visitors to the Delta or palaearctic migrants.

Seventeen range-restricted or biome-restricted species occur in the Okavango (Tyler and Bishop, 1998). One of these, the Chirping Cisticola is aquatic, and in Botswana is confined to the Okavango. The others are more widespread, and most are common in their respective habitats.

Following the criteria laid down by BirdLife International, the Okavango Delta is also of conservation importance for a substantial number of congregatory waterbirds; it supports over 1% of the global populations of 20 species, and 0.5% of the global populations of another 12 species.

Table 13. Globally threatened or near-threatened bird species occurring in the Okavango Delta.

Common name	Scientific name	Status
Vulnerable		
Slaty Egret	*Egretta vinaceigula*	Resident
Lesser Kestrel	*Falco naumanni*	Palaearctic migrant
Cape Vulture	*Gyps coprotheres*	Vagrant
Wattled Crane	*Grus carunculatus*	Resident
Corn Crake	*Crex crex*	Palaearctic migrant
Lappet-faced Vulture	Torgos tracheliotus	Resident
Near-threatened African Skimmer	*Rhynchops flavirostrisi*	Resident
Data deficient		
Black-winged Pratincole	*Glareola nordmanni*	Palaearctic migrant

The vast majority of the birds found in the Okavango Delta are breeding residents (339 or 76%) as shown in Table 14. There is, however, a significant number of palaearctic migrants all of which are waders (29.3%), that visit the Okavango specifically because of its wetland habitats.

Mammals

The Okavango Delta has a wide variety of large mammals occurring locally in high numbers, and which are the main attractions in the growing tourism industry (Mbaiwa, 2003). However, most mammals in the Delta are fairly small and often overlooked. The overall mammal biodiversity of this entire community is determined by such factors as habitat diversity, connectivity to species pools in the Southern African region and the environmental history of the Delta.

Number of species. Some 122 mammal species of 12 orders and 34 families live in the Okavango Delta (Table 15). All the larger species are wide spread across the African Savanna region. The distributional ranges of some of the larger mammals are marginally within the Delta. One of these, the Sable Antelope (*Hippotragus niger*), is common in the broad-leaved woodlands and the grasslands close to

Table 14. Numbers of resident and migratory bird species in the Okavango.

	Residents	Intra-African migrants		Palaearctic migrants	Status uncertain
	Breeding	Breeding	Non-breeding	Non-breeding	
No. of species	339	40	2	58	5
%	76.4	9.0	0.4	13.1	1.1

the Delta (Skinner and Smithers, 1990). Similarly, the Eland (*Taurotragus oryx*) and the Gemsbock (*Oryx gazella*) prefer drier landscapes and rarely spend time in the Delta (Skinner and Smithers 1990), while the White Rhino (*Ceratotherium simum*) was recently introduced after their local extinction (Mosojane personal communication, Botswana Department of Wildlife and National Parks).

Typical forest species do not occur in the Delta although the riverine woodlands in the Delta often have closed canopies. Their patchiness might be preventive for the establishment of such species. Similarly, there are no rocky outcrops in the Delta, so those mammals typical of this habitat such as the Klipspringer (*Oreotragus oreotragus*), the Rock Dassies (Procaviidae) and the Dassierat (*Petromus typicus*) are not found either. Some species that occur adjacent to the Delta in the dry Kalahari environment such as the Springbok (*Antidorcas marsupialis*), the Black-footed Cat (*Felis nigripes*), and the South African Hedgehog (*Erinaceus frontalis*) seem not to have been recorded in the Delta either. For these the wetter habitats here might be preventive. It is, however, difficult to understand why the typical South African mammal family with many species; the burrowing golden moles (Chrysochloridae), have not established themselves in the Okavango region. Similarly the Oribi (*Ourebia ourebi*) is missing, although it is common in the non-distant Chobe National Park and for which the Delta habitats seem to be suitable (Bonyongo, 2004).

Species composition and size distribution. Almost half of the mammal species are bats or rodents (n = 57). Most of these are small and weigh less than 100 g (Table 16). A third of the mammals (n = 40 species) are heavier than 10 kg and 11 of these are carnivores. At least 18 species weigh more than 100 kg. These include the large African antelopes, the Burchell's Zebra (*Equus burchelli*) and the African Lion (*Panthera leo*). The four species that are heavier than 1,000 kg include the White Rhinoceros, the Hippopotamus, the Giraffe (*Giraffa camelopardalis*), and the African Elephant.

The two most common of these megaherbivores (Owen-Smith, 1988) significantly affect the physical environment. Elephants that feed on a large variety of plants, including trees and shrubs, modify the terrestrial habitats of other species in the Delta (e.g. Gilson and Lindsay, 2003), for instance by changing woodlands to grasslands. Hippopotami on the other hand, change both the aquatic and floodplain habitats for species living in the Delta (McCarthy et al., 1998) by opening up channels and facilitating flooding.

Common species and total biomass. The Impala is the most common large mammal in the Delta (Table 17), followed by the Buffalo and the Red Lechwe (Bonyongo, 2004). Elephants are also very abundant. This species has increased in numbers from 2,300 (1975/76) to 5,700 (1984/85) (SMEC, 1989), 15,000 in 1988, and 35,000 in 2002 (Bonyongo, 2004). Similarly, the numbers of two other large herbivores, Hippopotamus and Buffalo, have increased remarkably during the last fifteen years, while most small and medium sized herbivores have declined (op. cit.). The abundance of elephants is now so high that they constitute a significant threat to woodlands, especially when considering that about 1/4 of the Delta is perma-

Table 15. Mammal orders, families and the number of species found in the Okavango Delta.

ORDER & FAMILY	COMMON NAME	SPECIES
Order Insectivora		**5**
Family Soricidae	Shrews	5
Order Macroscelidea		**1**
Family Macroscelididae	Elephant shrews	1
Order Chiroptera		**26**
Family Pteropodidae	Fruit bats	2
Family Emballonuridae	Tomb bats	2
Family Molossidae	Free-tailed bats	6
Family Vespertilionidae	Vesper bats	13
Family Nycteridae	Slit-faced bats	1
Family Rhinolophidae	Horseshoe bats	1
Family Hipposideridae	Leaf-nosed bats	1
Order Primates		**3**
Family Lorisidae	Bush babies	1
Family Cercopithecidae	Baboons & monkeys	2
Order Pholidota		**1**
Family Manidae	Pangolin	1
Order Lagomorpha		**1**
Family Leporidae	Hares	1
Order Rodentia		**31**
Family Bathyergidae	Molerats	1
Family Hystricidae	Porcupine	1
Family Pedetidae	Springhare	1
Family Gliridae	Dormouse	1
Family Sciuridae	Squirrels	1
Family Thryonomyidae	Canerats	1
Family Muridae	Rats & mice	25
Order Carnivora		**28**
Family Protelidae	Aardwolf	1
Family Hyaenidae	Hyaenas	2
Family Felidae	Cats	6
Family Canidae	Foxes & dogs & jackals	4
Family Mustelidae	Otters & polecat	4
Family Viverridae	Civets & genets & mongooses	11
Order Tubulidentata		**1**
Family Orycteropodidae	Aardvark	1
Order Proboscidea		**1**
Family Elephantidae	African elephant	1
Order Perissodactyla		**2**
Family Rhinocerotidae	Rhinoceroses	1
Family Equidae	Zebras	1
Order Artiodactyla		**22**
Family Suidae	Pigs	2
Family Hippopotamidae	Hippopotamus	1
Family Giraffidae	Giraffe	1
Family Bovidae	Antelopes & Buffalo	18

Table 16. Number of species in six body mass classes (kg) recorded for 12 mammalian orders in the Okavango Delta (Data from various authors in Skinner and Smithers, 1990).

	<0.1	0.1–1.0	1.1–10.0	10.1–100	101–1000	>1000
Insectivora	3	2				
Macroscelidea	1					
Chiroptera	23	3				
Primates		1	1	1		
Pholidota				1		
Lagomorpha			1			
Rodentia	24	5	1	1		
Carnivora		4	13	10	1	
Tubulidentata				1		
Proboscidea						1
Perissodactyla					1	1
Artiodactyla				8	12	2
Total	**51**	**15**	**16**	**22**	**14**	**4**

Table 17. Number of large mammals in the Okavango Delta in 2002, calculated for an area of 20,000 km^2, based on 10 aerial counts done 1988–2002 by the Department of Wildlife and National Parks, Government of Botswana (from Bonyongo, 2004). For Impala the numbers have been corrected based on ground counts.

Species	Total number
Elephant, *Loxodonta africana*	35,000
Zebra, *Equus burchelli*	14,000
Warthog, *Phacochoerus aethiopicus*	2,000
Hippopotamus, *Hippopotamus amphibius*	2,500
Giraffe, *Giraffa camelopardalis*	5,000
Wildebeest, *Connochaetes taurinus*	8,000
Tsessebe, *Damaliscus lunatus*	3,000
Impala, *Aepyceros melampus*	140,000
Buffalo, *Syncerus caffer*	60,000
Kudu, *Tragelaphus strepsiceros*	300
Sitatunga, *Tragelaphus spekei*	500
Red Lechwe, *Kobus leche*	60,000

nently wet (P. Mundy, pers.comm.). The Hippopotamus numbers given at about 2,500 are likely to be a minimum, due to the problems in aerial counting of these often submerged animals. For similar reasons the numbers based on aerial counts given in Table 17 for Sitatunga and Kudu, are likely to be very under-estimated. The numbers derived by aerial counts for Impala are very under-estimated as well, but here it has been possible to correct for this error by integrating the relationship between aerial and ground-truthed density estimates (Bonyongo, 2004).

The total mammal biomass for the Moremi Game Reserve (7,000 km^2) in the Okavango Delta has been estimated as being 12,000 kg/km^2 (Bonyongo, 2004), which is much higher than for most wildlife areas in southern Africa and comparable with the rich savannas in the East African Rift valley. Compared with regression models between rainfall (Coe, Cumming and Phillipson, 1976) and rainfall + nutrient level (East, 1984) the Okavango wildlife biomass is 4–8 times higher than expected. The extended productive period caused by the annual flood is certainly one of the causes for this. On the other hand the generally low nutrient levels in the Delta should limit biological production (op. cit), but the dynamic vegetation successions caused by flooding with periodically and locally high mobilization of nutrients may cause high nutrient levels for forbs and hence favorable production conditions for grazing mammals.

Habitat assemblages. All the common species mentioned above, except the Buffalo, depend on more than one habitat. For instance, the Impala inhabits floodplains and grasslands adjacent to riparian woodlands, while the Red Lechwe prefers the seasonal floodplains close to deeper waters of the Delta (Skinner and Smithers, 1990). The Hippopotamus grazes at night often several kilometres from the rivers and lakes which it uses during the day (Skinner and Smithers, 1990). Elephants are also water dependent. They are mixed feeders and use most of the habitats in the Delta (op. cit.).

There are some clear differences in species composition along the wet-dry habitat gradient in the Delta. The Hippopotamus, the Sitatunga, the Cape Clawless Otter (*Aonyx capensis*) and the Spotted-necked Otter (*Lutra maculicollis*) live in the deeper, usually permanent waters of the rivers, lagoons and lakes (Skinner and Smithers, 1990). The Reedbuck (*Redunca arundinum*) occurs in the seasonally flooded areas with lower Cyperaceae species, while the Red Lechwe frequents the floodplain grasslands in large numbers (Skinner and Smithers, 1990). These wet habitats support 3 and 21 species each (Table 18) each, and are different in species composition from each other and from the drier habitats. They have a high proportion of grazers while insectivores (mainly bats) are absent.

The drier habitats across the Delta (riverine forests, riverine woodlands, savanna woodlands, dry woodlands and dry scrub), on the other hand, support similar groups of species (Table 18). These habitats are more species-rich with a total of 110 species (Table 18) and with a

typical mammal composition of the East-South African savannas. These include the big cats (Lion, Leopard (*Panthera pardus*) and Cheetah (*Acinonyx jubatus*) which are common as well as the Spotted Hyaena (*Crocuta crocuta*); and the endangered African Wild Dog (*Lycaon pictus*) has a stronghold here. The large number of species is due to the species-rich groups of bats and rodents (Table 15) which predominantly occur here. The most common herbivores are listed in Table 17. It is obvious that these woodlands provide habitats for a larger number of frugivores, browsers, granivores and insectivores than the open sedge- and grasslands (Table 18).

The diversity of the habitats over relatively small areas in the Delta should enhance the number of species (Rosenzweig, 1995). Bonyongo (2004) has corroborated this further. He found a highly significant positive regression between habitat heterogeneity for five large protected areas in southern Africa – including the Okavango Delta – and their herbivore species richness.

Reproduction. In the Southern African region at least 75% of the species living in the Okavango Delta give birth during the summer months (Smithers 1971; 1983), while six species breed during winter only. These same species breed during winter in the Delta as well (Table 19). In the Delta, however, another 12 species are winter breeders which are summer breeders in the region and an additional 27 species are winter breeders which breed year round in the region. This might indicate that the prolonged breeding is a response to the relative predictability in abundance of resources during the flooding.

Discussion

Species and habitat richness

As the number of species increases with size of the study area following a log/log relationship (see Rosenzweig (1995) for an overview), a proper comparison of biodi-

Table 18. Habitat-specific number of species recorded in functional trophic groups for nine broadly defined habitat types in the Okavango Delta.

	Swamp	Reedbed	Aquatic grass	Grassl.	Riverine forest	Riverine woodl.	Savanna woodl.	Dry woodl.	Dry scrub
Insectivores	2	2	3	1	8	13	29	10	8
	14%	17%	19%	3%	32%	31%	33%	32%	24%
Herbivores	8	6	8	17	8	13	31	15	12
	57%	50%	50%	53%	32%	31%	35%	48%	35%
Frugivores	–	–	–	–	2	2	1	–	–
Browsers	1	1	1	1	5	6	5	5	2
Granivores	2	–	1	4	–	5	7	5	4
Grazers	6	4	4	14	–	1	15	4	5
Tuberivores	–	–	–	–	1	1	1	1	1
Carnivores	2	2	3	7	4	7	14	10	9
	14%	17%	19%	22%	16%	17%	16%	32%	26%
Omnivores	2	2	2	7	5	9	14	6	5
	14 %	17%	13%	22%	20%	21%	16%	19%	15%
Total	**14**	**12**	**16**	**32**	**25**	**42**	**88**	**31**	**34**

Table 19. Comparison of seasonal breeding patterns for mammals in the Okavango Delta with that of the Southern African region.

	Winter breeders in SA region and Delta	Summer breeders in SA region and winter breeders in Delta	Whole year breeders in SA region and winter breeders in Delta	Same breeding in SA region and Delta or unknown
Insectivora		2	1	2
Macroscelidea				1
Chiroptera				26
Primates		2		1
Pholidota	1			
Lagomorpha			1	
Rodentia		6	7	18
Carnivora	4	1	5	18
Tubulidentata		1		
Proboscidea				1
Perissodactyla			1	1
Artiodactyla	1		12	9
Total	**6**	**12**	**27**	**77**

versities between the Okavango Delta and other areas in the region requires that this relationship is known for each taxonomic group. This is, of course, not the case. A crude comparison is nevertheless attempted in Table 20 between the Okavango Delta and the countries in the Southern African region. The calculated total number of species per one square kilometer for the Okavango Delta, 329 for the six biological groups, is slightly higher than for Botswana, probably reflecting the larger contribution of aquatic species. The species density, however, decreases within the dry part of the gradient and is considerably lower than for the wetter countries to the north with values of 500–700 species per km^2. South Africa stands out with a much higher species density which is caused by the extremely species-rich Cape Floral kingdom. With the exception of this unique area, the species richness in the Okavango Delta is in the range of the other biomes in the southern part of the Southern African sub-continent.

The species rich Odonata fauna is probably a true feature of the Okavango as this group is well studied in the region. The large variety of aquatic habitats may be the reason.

The number of habitats identified in the Delta is not significantly higher than in the surrounding Kalahari. The density of habitats, with as a mean 5–6 habitats repeated 30–36 times in each area of 9 km^2, may however be high. Comparisons with other data are difficult since it is hindered by the particularities of the habitat classification used. A high number of habitats per area will give a high "edge effect" (*sensu* Leopold) which in turn will favor species that are using more than one habitat. The high density of Impala which is the most numerous antelope in the Delta and uses the woodland-grassland inter-phase, may be an example of this edge effect.

The highest habitat density occurs at the Delta fringes (Fig. 5), where the hydrological gradients are likely to be steepest and have the widest total range. These are, therefore, also the areas which probably have the highest total biodiversity and those species which are dependent on more than one habitat for their development or their daily activities will be particularly favored here. This is a new insight that challenges the conservation efforts of the Delta (see below).

Flooding, productivity and habitat succession

There are two major processes organizing productivity and habitat succession in the Okavango Delta: Firstly the flood pulse without which the seasonal floodplains with its entire flora and fauna would disappear, and biological productivity would be dramatically reduced. The second process is the shift in flood distribution over different time scales. This creates a dynamic patch system of different nutrient levels and at different stages of biological succession (Fig. 8). During a flooding phase – irrespective of long or short – there is an accumulation of dead organic matter. If permanently wet conditions continue for years and decades a layer of peat will accumulate and keep nutrients such as phosphorus inaccessible in the organic matrix. When dry conditions reoccur due to drought or river avulsion which moves the flooding elsewhere, the peat will be oxidized by fire or microbes and the nutrients released. A highly productive grassland is formed which will attracts grazing wildlife and livestock as well as alert agriculturalists. The high wildlife biomass in the Delta of 12,000 kg/km^2, which is about six times higher than expected (Bonyongo, 2004), indicates the importance of the mobilization of nutrients for biological productivity. This is, of course, also caused by the direct effect the annual flood has on the production of grazing for herbivores. Similarly, this flood is significant for the annual cycle of aquatic productivity by causing the high nutrient levels, with resulting high zooplankton- and fish production on seasonal floodplains (Högberg et al., 2002). As the soils are composed of fine sand, the mobilized nutrients will not be retained easily on site, but disperse gradually and

Table 20. Number of species in different groups in the Okavango Delta (from this study and for Odonata from Kipping, 2003), as compared with other countries in the region (from Cumming, 1999).

	Okavango Delta	Botswana	Angola	Namibia	South Africa	Zambia	Zimbabwe
Area 10^3 km^2	25	600	1,247	824	1,221	752	390
Mammals	122	154	276	154	247	229	196
Birds	444	569	872	640	774	732	634
Reptiles	64	143	150	140	301	160	156
Amphibians	33	36	80	32	95	83	120
Odonata	94	114	250	117	147	222	157
Fish	71	81	268	97	220	156	132
Flowering Plants	1,300	2,000	5,000	3,159	20,300	4,600	6,000
Plant density per 1 km^2	210	182	400	272	1,629	403	591
Total (excl. Odonata)	2,034	2,983	6,646	4,222	21,937	5,960	7,238
Total species density (excl. Odo.) per 1 km^2	329	285	531	364	1,761	522	713

Note: The species density has been calculated using the same formula as in Table 4.

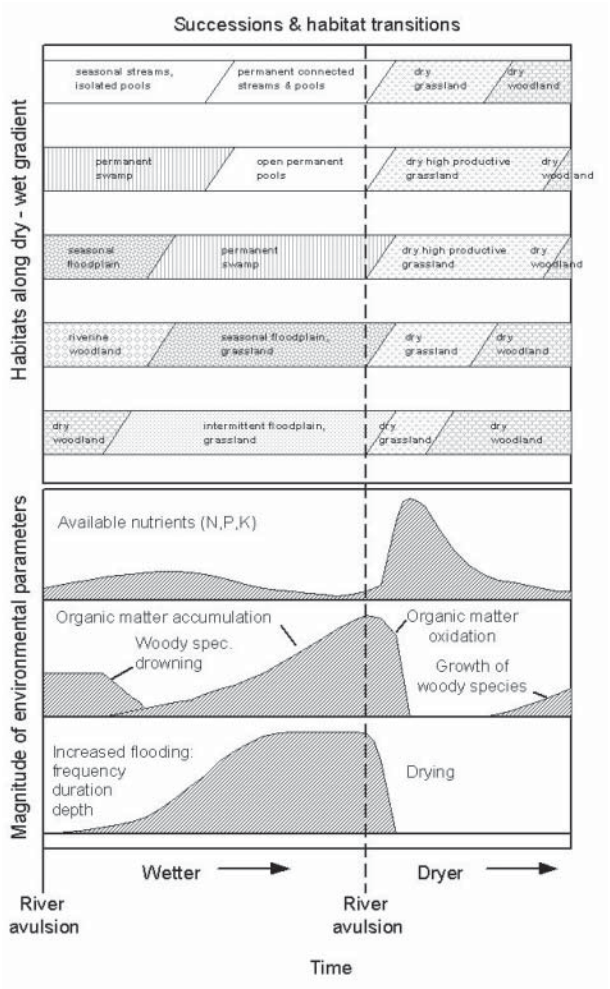

Figure 8. The principal habitat successions in the Okavango Delta following an initial period of increased flooding and after a time span of decades to centuries a shift to a drying phase. The bottom part of the figure illustrates how organic matter and nutrients accumulate, mobilize and disperse during such a sequence. The upper part illustrates how communities along a typical wetland gradient will change during this sequence.

hence the fertile grassland will become more and more nutrient-poor and eventually become encroached by woody species and end up as a dry woodland-bushland. Sooner or later the flood will return and drown the trees and again form the typical wet-dry gradient from permanent streams, lagoons and sedge-lands over seasonal grasslands to riparian woodlands. This ever changing system of biological successions is caused by three factors: The fact that the Delta is a slightly conical alluvial fan causes a lack of spatial stability of stream channels; the substantial sediment transport in the stream channels in the Delta, causes blockages and forces the water to flow into other areas (McCarthy and Ellery, 1998); and the predictable seasonal flood pulse that is the direct factor leading to flooding of large areas, but in turn depends on the rainfall pattern in the Angola highlands and the hydrographic characteristics of its drainage basin and river channels. In combination these geophysical, hydrological and meteorological factors create the unique Okavango Delta biological landscape.

Speciation and biogeography

There are at least four factors which should enhance the evolution of new species in the Okavango Delta. In its present phase it is almost entirely isolated from other wetlands and is an oasis in the huge Kalahari dry savanna. It has a unique hydrology with flooding during the cold season, while usually in the tropics and sub-tropics the cold season is also the dry one. In these areas the warm season is also the wet one, often with torrential rains and flooding. This is the case in the Delta as well, and therefore it has two wet periods with high biological production. Due to a pronounced continental climate the shallow waters on flood plains at an elevation of about 1,000 m asl often freeze during the cold season. There is no other large wetland in the Southern African region with this combination of features. Finally, most aquatic and wetland species in the Delta: fishes, snails, odonates, amphibians, reptiles (the aquatic and wetland species), originate predominantly from the north and more or less tropical environments and are likely to be less well adapted to the specific Delta environment, and thus are probably under evolutionary pressure to adapt. An indication of ongoing evolutionary changes may be that a considerably larger proportion of mammal species as compared to the Southern African region are winter breeders here, which is probably an adjustment to exploit the high biological production during the cold flooding season. As mating for most of these species takes place a year to a month before the flooding arrives – which thus cannot trigger reproduction – it is likely that genetic mechanisms have already evolved.

There are, however, no confirmed endemic species in the Okavango Delta. This is probably due to a combination of geographic features and climate variability. The interior central part of southern Africa with the upper Zambezi and Okavango Rivers is an ancient highland plateau at about 1,000 m asl with extremely low gradients. Over a distance of more than 500 km from the Liuwa floodplains downstream (Fig. 1) the gradient is 1:10,000. The flow in the hydrological connection (the Chobe tributary) between the Okavango Delta and the Zambezi, can go in either direction depending on which of the rivers has the highest water level (Davies, 1986). Although the longterm climatic variations are not known in detail, it is certain that there have been very dry periods as evidenced by fossil sand-dunes around the Okavango Delta as well as wet periods indicated by widespread alluvia extending from the Delta and into the Zambezi (see Mendelsohn and el Obeid, 2004). Several such climate

Table 21. Number of species in taxonomic groups of originally terrestrial origin observed in each major habitat in the Okavango Delta. For plants and mammals the data is for actual number of species observed in each habitat i.e. overlapping species are included, whereas for reptiles and birds the data is based on the authors' classification of species into either aquatic-, wetland- or dry land – whereby habitat overlapping is excluded.

Taxonomic group	Number of species	Sum observed in each habitat	Percent habitat overlap	Aquatic/ Perennial swamp	Wetland/ Seasonal swamp	Dryland/ Terrestrial
Plants (1)	1,061	1,428	35 %	205	519	704
Reptiles (2)	64			7	5	52
Birds (3)	444			112	57	275
Mammals (4)	122	134	10 %	3	21	110

(1) Data from Smith (SMEC, 1989).
(2) Data from this study but observations per habitat are missing.
(3) Data from this study but observations per habitat are missing.
(4) Data from this study.

swings have probably taken place during the last 100,000 years. The Okavango Delta has thus been fairly isolated from the Zambezi system in dry periods and perhaps even completely dried out, while in wet periods it was probably part of a huge wetland complex of several 100,000 km^2 which occupied the central and southern part of western Zambia, southwestern Angola, the Caprivi strip in Namibia and northern Botswana with the Okavango Delta and the Makgadikgadi Pan (Fig. 1). The high connectivity between the Okavango and the Zambezi is indicated by the large similarities between them in species composition of many aquatic biological groups such as amphibians, fish, dragonflies and mollusks.

During transitional periods changing from dry to increased wetness the Delta expanded and established an irregular link with the Zambezi system. Few individuals of wetland species may have dispersed through this narrow pathway and found an environment with unused or under-used niches which are not identical to the ones of their origins. This is a situation of *competitive speciation* (Rosenzweig, 1995), which is a comparatively fast process. However, in the next phase when the Delta became a part of a large wetland system with an easy migration of species and flow of genes, it is likely that the newly established genetic diversity – probably mainly below species level – merged with the larger gene pool of the species and thus cannot be detected. Although *geographical speciation* is expected to occur in this large wetland complex with an open flow of genes, the rate of speciation in this period was probably low (Rosenzweig, 1995). During periods of receding wetlands on the other hand, many niches decreased in their extent, the competition became more intense and the risk of extinction increased. These processes may explain the low degree of endemism in the Okavango Delta. However, for a better understanding both the frequency of climate changes and the rates of speciation must be known.

The larger Okavango-Zambezi wetland complex, on the other hand, has a fair number of endemic species. White (1983) defined the Zambezi phytochorion based on more than 50% endemic plant species and also identified the "Barotse Centre of Endemism" (White, 1965) basically identical in extent with the huge wetland complex described above. The whole antelope sub-family Reduncini, which is almost entirely confined to African wetlands, has a high biodiversity in this area with four biological species and more than ten mostly endemic subspecies (Cotterill, 1998). Similarly, 23% of all fish species in this wetland complex are endemic, and more than half of them originate from the Congo River system to the north, where the Zambezi has tapped into several river systems and thus expanded its catchment (Skelton, 1993). This tropical origin of species is likely to also be the case for many other groups of aquatic biota, especially because the Kalahari to the south has formed a formidable migration barrier for a long time.

The uniqueness of the biology of the Okavango Delta landscape is intuitively felt. It is, however, not caused by the occurrence of endemic species nor a high diversity of species. These features are normal for the Southern African region. Two other factors, however, may be more unique: Habitat density – not the number of habitats – is probably high resulting in a high "edge effect" (*sensu* Leopold) which favors species using more than one habitat. Secondly, and probably more importantly, the biological productivity, best reflected in the very high biomass of large mammals, is much higher than expected. This is in all likelihood caused by the large scale shifts in flooding patterns over time in combination with the annual flood-pulse; mechanisms that both accumulate and mobilize nutrients.

Threats to biodiversity

Development and planning in most human societies strive towards stability and predictability, which in the case of the Okavango Delta is in direct conflict with its inherently unstable nature. There are several examples where the lack of understanding the Delta's nature has caused concerns. Inside the Delta the channelling of water, clearing and dredging of waterways have been done in the past and are still being proposed even now by the Department

of Water Affairs, Government of Botswana (Ramberg 2002; 2004b). The largest scheme of this kind "the Southern Okavango Integrated Water Development Project" (1985–92) was finally canceled after a seven year planning period and a cost of many million dollars due to strong local opposition and a critical international review (IUCN, 1993).

Upstream of the Okavango Delta, Namibia has fairly large plans to pump water from the river for irrigation, and in Angola there are a number of (old) plans for the construction of as many as 16 hydro-electrical power plants (Mendelsohn and el Obeid, 2004). If implemented, these schemes are likely to have severe negative impacts on the bio-diversity of the Delta since they will reduce both the total inflow and the peak flows and thus the extent of the flooded areas. In addition, dam operation will level out discharge variability, cut off flood flows and again reduce the flooded areas (Ramberg, 1998). Due to the trapping of sediments in the reservoirs the frequency of shifts in flooding locations will also be reduced. The river avulsions driving these changes during floods are caused by transported silt and sand, which eventually settle as sediment in the Delta channels building up channel blockages (McCarthy, 1992), resulting in shifts of the channel network.

The highest habitat diversity is found in the fringe areas of the Delta. As discussed above, it is of course also highly likely that total species diversity is highest here. The highest losses of species are, therefore, likely to be caused by the first water development schemes. The implications for the management of biodiversity in the Delta are immense since it cannot be concentrated on preserving some kind of core area, and is complicated even more by the fact that these fringe areas with highest biodiversity are under strongest local human exploitation pressure as well.

There are other threats to the biodiversity of the Delta, in particular from the livestock industry which – through the Ministry of Agriculture – were responsible for the aerial spraying against tsetse flies (Perkins and Ramberg, 2004a, b). This might have caused a loss of invertebrate species as indicated by the reduced number of dragonfly species over the past 30 years and the disappearance of many invertebrates after the recent spraying. As usual in such cases, the lack of background and benchmark data makes the results inconclusive. The Ministry of Agriculture has also constructed "veterinary fences" to prevent transmission of diseases from wildlife to livestock, which have effectively blocked the migratory routes for mammals between the Delta and the Kalahari (Conservation International, 2003). This has probably been decisive for the observed reduction of wildlife numbers in the whole north-western Botswana.

The forces counteracting all these eager developers are the thriving and developing tourism industry, for which a pristine Okavango Delta is vital, and the international conservation forces. The tourism industry in the Okavango Delta is hampered by the same weaknesses as in Africa in general (Ramberg, 1993); the benefits to local populations are comparatively small and consequently it has weak local political support, while the livestock sector which is competing for land is well embedded in the local and central governance structures. The international interests in the conservation of the Delta were boosted when the Government of Botswana ratified the Ramsar Convention in 1997 and designated the Okavango Delta "a wetland of international importance". This was as a direct response to the threat from Namibia to draw water from the river through a pipeline to its capital Windhoek (Ramberg, 1997). In particular the Ramsar bureau and IUCN have worked for a management plan for the Delta together with the Government of Botswana. For management of the entire river basin the three countries, Angola, Namibia and Botswana have established a joint commission, OKACOM (Permanent Okavango River Basin Commission) in 1994 which has been fairly passive up to now, probably due to the civil war in Angola which ended in 2002. Recent international support has revitalized the organization which will now embark on the development of a joint management plan for the whole river basin.

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