Swamps of the Upper White Nile

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Abstract The Sudd swamps developed from a large lake which extended north to Khartoum during the Pleistocene. The main channels are stable over decades, but the bends show upstream migrations of about 20 m in 3 years. In permanent swamps the channels often have a band of *Vossia*, backed by papyrus, which in turn is backed by an extensive area of *Typha domingensis*. Before 1950 the Nile Cabbage, *Pistia stratiotes*, was an important part of the floating vegetation in permanent swamps, but in recent years it has been largely replaced by *Eichhornia crassipes*.

Seasonal flooding enables the growth of grasses such as *Echinochloa* spp. and *Oryza longistaminata*. Further from the channels, where rain is the main source of water, *Hyparrhenia rufa* is the main grass. The grasslands grade into open woodland with *Acacia seyal* and *Balanites aegyptiacus*.

A rich fauna was associated with *Pistia*, and a similarly rich fauna has developed around the invasive *Eichhornia*. The marginal vegetation shelters an association of microcrustacea, with a biomass 100 times that in the open water. Macroinvertebrates are also abundant and diverse; for instance there are at least 70 species of aquatic Coleoptera, 60 species of mosquitoes, and a special fauna of terrestrial forms occurs in the umbels of papyrus. About 68 species of fish occur, and they occupy a wide range of niches, from mud feeders to carnivores.

Mammalian swamp dwellers include *Hippopotamus*, and several antelopes such as the Sitatunga and Nile Lechwe, while the White-eared Kob makes large migrations in the seasonal grasslands.

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1 Introduction

The swamps of southern Sudan are centred on the triangle formed by the Bahr el Ghazal, flowing west to east, the Bahr el Zeraf, and the Bahr el Jebel (or Gebel), flowing from the south to north. The junction of the last two rivers is via the man-made Zeraf cuts. The swamps extend southwards along the braided Bahr el Jebel, reaching just beyond Bor. The Bahr el Ghazal is fed by numerous tributaries, mostly arising on the Congo-Sudan divide. Many of these tributaries are seasonal, but the Sue, which flows into the Jur, reputedly flows throughout the year. A good account of the early exploration of the waterways in this area is given by Christie (1923). On the eastern side the Nile is joined by the Sobat, which receives tributaries from highlands on the borders of Ethiopia. The enormous extent of this area is indicated by the width of Fig. 1 representing approximately 1,300 km, which is about the distance from London to Vienna.

These swamps are known as the Sudd, a name derived from the Arabic for a blockage, and originally applied to the barriers formed by floating papyrus, but the term Sudd is now more widely used in other parts of Africa to include any type of mat-forming floating vegetation (Thompson, 1985).

A vast amount of information on topography, climate, hydrology, vegetation and human geography is contained in the four volumes of the report of the Jonglei Investigation Team (JIT, 1954). In addition, the four volumes produced by Mefit-Babtie (1983) take into account the changes in hydrology since the exceptional rains of 1961–1962. Much of this information was gathered in relation to the proposed construction of the Jonglei Canal, which has been discussed in detail in the book edited by Howell et al. (1988). The present chapter will not consider the Jonglei Canal

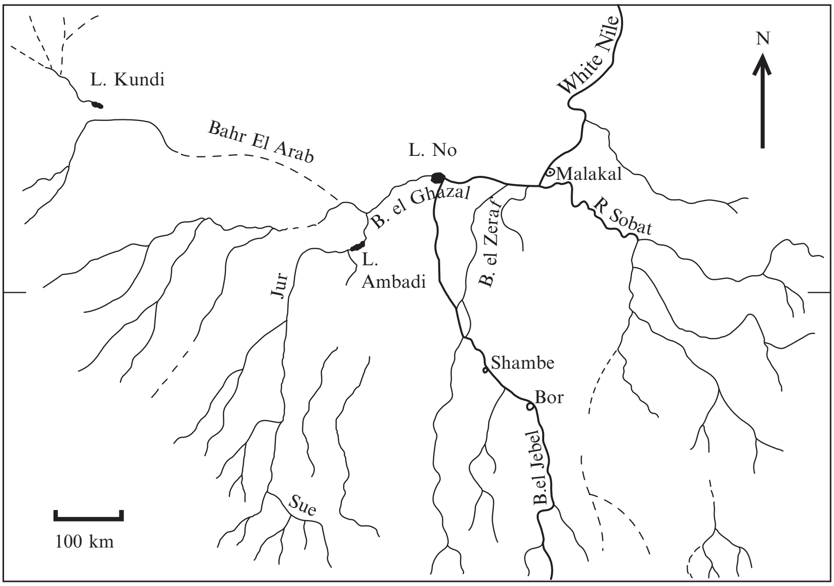

Fig. 1 Map of the upper White Nile showing the main localities mentioned in the text. Note the scale

(construction of which is at present incomplete), but instead will concentrate on the biological communities in the swamps, and the conditions under which they survive.

Talling (1957) made a major study of the succession of water characteristic along the White Nile. Two surveys were made: one in June 1954, the second in December 1954. In both there were decreases in dissolved oxygen and pH as the water entered the Sudd, with a gradual recovery after leaving the swamp. Differences in inorganic phosphate were found between the surveys, with roughly twice as much present in June. Ammonia and nitrate were also more abundant in June. Data for sulphate were available only for December, but showed the most clear-cut effect of passage through the swamp, with a marked decrease that was not followed by any significant recovery. This result was attributed to the activities of sulphate reducing bacteria in low oxygen concentrations.

2 Origin and History

The Lake Sudd hypothesis envisaged a huge lake, extending from Juba to Khartoum (Lombardini, 1865; Lawson, 1927; Ball, 1939), but Whiteman (1971) reviewed evidence for a much smaller lake, extending southwards from Khartoum. He obtained radiocarbon dates of 11,300 and 8,730 BP from shell bearing deposits, which indicated that during that period the water level near Khartoum was up to 10 m above the present flood level. The present Sudd swamps are a relict of a Pleistocene lake that covered a larger area, and extended further north than at present. The change from lake to swamp started with the onset of drier conditions about 4,000 BP. There are still numerous areas of open water: and some, such as Lake Shambe, have areas up to 30 km^2.

3 Vegetation

The distribution of swamp vegetation varies over time. Lock and Sutcliffe (1988) give three maps for the years 1930, 1952 and 1983 showing how the permanent swamp expanded from 6,700 km^2 in 1952 to 19,200 km^2 in 1983. This expansion was linked to the exceptional rains of the early 1960s and the raised discharge from Lakes Victoria and Albert. Apart from this general expansion there are detailed local changes in the channels and smaller lakes. Petersen et al. (2007) examined satellite pictures taken in 1973, 1979, 1987 and 2002 of the region between Bor and Shambe. They found that the main channel system was fairly stable, but the bends showed upstream movements of about 200 m over the 30 year period. The lakes were stable in location, but some showed significant reductions in area. Between 1973 and 2002 the surface area of Lake Shambe decreased from 30 to 27 km^2. Over a different timescale, between 1930 and 1981, in the southern part of the swamp, a new lake system appeared at Wutchung (Lock & Sutcliffe, 1988).

In spite of such physical changes there remains a fairly consistent pattern in the vegetation. Along the main channels there is often a *Vossia* swamp, forming floating mats. Before the 1950s the Nile Cabbage, *Pistia stratiotes*, was associated with this region, but it has since been replaced by *Eichhornia crassipes*, which can form a broad band in the more sheltered regions. Behind the *Vossia* there is an extensive area of *Cyperus papyrus*, usually forming a floating mat, often strong enough for a man to walk on. The tall plants form a framework for climbers, such as *Luffa cylindrica* and *Vigna luteola*, while the umbels provide shelter and food for a range of terrestrial insects and arachnids. In some areas the papyrus is replaced by the tall reed *Phragmites karka*, which does not form a floating platform. Further away from the main channels there are swamps dominated by *Typha domingensis*, which occupy three times the area covered by papyrus. These *Typha* swamps are difficult of access and little studied.

During the wet season, water spills out from the permanent swamps and floods nearby grasslands. Where the water is deeper the wild rice-grass, *Oryza longistaminata*, is dominant. Its success depends on the duration of flooding, as it requires several months of surface water in order to flower. Where the floodwater is shallower the dominant grass is *Echinochloa pyramidalis*, which may be accompanied by *Sporobolus pyramidalis*, *Digitaria debilis*, and legumes like *Desmodium hirtum*.

In the area of seasonal flooding from the river there are slightly deeper areas, which persist as pools as the water recedes. These pools can develop their own separate vegetation, consisting of the grass *Echinochloa stagnina*, small herbs, such as *Glinus lotoides*, and sometimes woody species like *Sesbania rostrata* and *Aeschynomene indica*.

Beyond the flooding by the river there is an area seasonally flooded by rainfall. *Hyparrhenia rufa* covers most of this area, although *Sporobolus pyramidalis* can also dominate in some areas, and where the soil is better drained, *Echinochloa haploclada* becomes important. There is of course no sharp distinction between river flooding and rain flooding, so areas inundated by the river can receive additional water from rainfall, and this is important in maintaining the seasonal pools.

The grasslands merge into open woodland, characterised by the red barked *Acacia seyal* and the larger, grey-brown barked *Balanites aegyptiaca*. These trees can be killed off if they are flooded for a long time, and the maps given by Lock and Sutcliffe show that woodlands disappeared from some areas between 1952 and 1983, when the permanent swamps expanded. Regeneration of woodland occurs after several years without flooding, and may have unwelcome consequences for the local tribes. Ashford and Thomson (1991) regard the regeneration of *Acacia*/*Balanites* woodland as the key event in an epidemic of visceral leishmaniasis, because the young woodland provided a suitable habitat for the sandfly vector *Phlebotomus orientalis*.

4 Fauna Associated with Floating Macrophytes

Perhaps the most striking change that has taken place between the survey by Migahid (1948) and the later surveys by Denny (1984) and Lock (1988) is the replacement of *Pistia stratiotes* by *Eichhornia crassipes. Pistia* provided a floating rosette with a mass of roots extending down into the water. In 1954, Ian Thornton made a study of the animals associated with *Pistia*, and his results were presented by

Rzóska (1974). The complex fauna included Diptera, Ephemeroptera, Hemiptera, Odonata, Trichoptera, Coleoptera, Hymenoptera (mainly ants on the aerial rosette), Araneida, Acarina, Crustacea, Gastropoda, Hirudinea and Oligochaeta. One individual plant could harbour up to 300 animals, particularly on the fringe of a patch where oxygen was available. Coleoptera were particularly abundant, and included over 40 aquatic species. The Crustacea included a small decapod, *Caridina nilotica*, and the conchostracan *Cyclestheria hislopi*.

A parallel study of the fauna of *Eichhornia* in the Sudd has been made by Bailey and Litterick (1993). They found that *Eichhornia* effectively provides the same niches as those provided by *Pistia*. Coleoptera were again the most abundant group, with about 30 aquatic species, but rather surprisingly only about five species were the same as those found on *Pistia*. This implies a pool of at least 70 species of aquatic Coleoptera in the Sudd. The crustaceans *Caridina* and *Cyclestheria* apparently transferred to the shelter provided by *Eichhornia* and became important members of the community associated with that plant.

Numerous small crustaceans are associated with the marginal vegetation. Rzóska (1974) found 34 species of Cladocera, and Monakov (1969) gives biomass figures for microcrustacea in fringing vegetation up to 100 times higher than in the open water. Among the copepods Rzoska lists *Mesocyclops leuckarti*, but this was before the revision of the African species of *Mesocyclops* by Van de Velde (1984). More recent surveys (Mefit-Babtie, 1983) show *Mesocyclops ogunnus* in the lake at Wutchung, *M. rarus* in the River Atem, and *M. salinus* in seasonal pools. *Thermocyclops neglectus* appears to be the most widespread of the cyclopoids in the swamps.

5 Zooplankton

Away from the marginal vegetation the crustacean zooplankton becomes sparse and poor in species. Table 1 shows the species present in Lake No in January 1949 and April 1978. The overall composition of these samples forms a contrast to those from Lakes Albert, Edward and Victoria, where the percentage of cyclopoid copepods is very much higher.

Table 1 Percentage composition of crustacean zooplankton in Lake No

	January 1949[a]	April 1978[b]
Diaphanosoma excisum	2	10
Daphnia barbata	0	1
Ceriodaphnia dubia	0	1
Moina micrura	54	8
Bosmina longirostris	0	2
Thermodiaptomus galebi	21	62
Cyclopoida	12	15
Others	11	1

[a] Data from Rzóska (1974).
[b] Data from Green (1984).

Information on the Rotifera present in the Sudd has been provided by De Ridder (1984), based on samples collected by A. I. El-Moghraby, and by Green (1984), plus identifications in Mefit-Babtie (1983). Combining these three sources gives a total of 86 species found in the area shown in Fig. 1. More species will certainly be found. For the whole of Sudan, De Ridder (1984) lists 145 species, most of which are likely to occur in the Sudd. The commonest species in the open water are *Brachionus calyciflorus*, *B. caudatus*, *B. falcatus* and *Keratella tropica*, while *Lecane bulla* is the most frequent of the 26 species of *Lecane* recorded from the Sudd. The small pools that develop in the flooded grassland during the wet season have a rich association of rotifers, with about 30, mostly periphytic, species. They include the rarely recorded *Pseudoploesoma greeni*, which is not listed by De Ridder, but also occurs in Lake Ambadi. The peculiar nature of the rotifer association in Lake Ambadi has been discussed by Green (1984). Although rotifers are sparse in the lake their index of diversity (α) is much higher than elsewhere in the Sudd. A similar high diversity is found among the desmids in Lake Ambadi (Grönblad et al., 1958), and this was thought to be unique, but the pools in the grasslands also develop a rich association of desmids. Although a detailed comparison has not been made, the desmids in the pools appear to be dominated by species of *Closterium* and *Cosmarium* (Mefit-Babtie, 1983).

6 Macroinvertebrates

The macroinvertebrates in the Sudd near Bor have been listed in Vol. 3 of the Mefit-Babtie Report. Five species of Ephemeroptera, including the tunnelling larva of *Povilla adusta* were found, but only two species of Trichoptera are listed. The Odonata were much more abundant, with 24 species, and there were 30 species of Coleoptera. Sixteen species of aquatic Hemiptera are listed, but this is probably an underestimate, since Linnavuori (1971) listed 38 species from the province of Bahr el Ghazal, and some additional species from Equatoria. There are only eight species common to both lists, so there must be over 45 species of aquatic Hemiptera in the Sudd.

About 180 species of mosquitos are known from the Sudan, and at least 60 of these occur in the Sudd, including five species of *Taeniorhynchus*, the larvae of which become closely connected to vegetation by piercing plant tissues with saw-like siphons to gain access to air spaces. This enables the larvae to remain permanently underwater when there is little dissolved oxygen.

The Mefit-Babtie Report lists 14 species of gastropods, although Brown et al. (1984), working in the same area found 23 species, including the transmitters of schistosomiasis, fascioliasis and amphistomiasis. The large snails of the genera *Pila* and *Lanistes* are often found in the seasonal pools in the flooded grasslands, where they survive the dry season by aestivating. They form a large part of the diet of *Anastomus lamelligerus*, the Open-bill Stork.

An unexpected inhabitant of the Sudd is the hydroid *Cordylophora*, which is widespread in brackish water through out the world, but is also known from freshwater, though rarely so deep into a continent (Rzóska, 1949).

7 Upland Tributaries of the Bahr el Ghazal

As one travels upstream on the tributaries of the Bahr el Ghazal towards the Congo/Sudan divide the slopes become steeper, and the riverbeds rockier, eventually they become bare of vegetation, apart from an occasional species of Podostemaceae (Schweinfurth, 1873). This is reminiscent of the streams on Mount Elgon, and it is probable that the tributaries of the Bahr el Ghazal have a similar invertebrate fauna, although it has not been studied to the same extent. One group, the blackflies (Simuliidae), because of their importance as transmitters of disease, has been studied in detail (Lewis, 1948, 1952, 1953). Of the 22 species Lewis records from the Sudan, nine also occur on Mount Elgon. Some of these species are widespread in the Nile, but others are restricted to the upper reaches of the Ghazal tributaries. An extreme example is *S. lepidum* which is abundant only at the base of the Aga Falls at 1,100 m asl. *Simulium damnosum* is well known as a transmitter of the nematode *Onchocerca volvulus*, which causes river blindness, and the main area of transmission in the Sudan occurs along the Rivers Jur, Sue and nearby tributaries.

8 Fauna of Papyrus Umbels

The umbels of papyrus open well above water level, so one would expect the animals living there to be predominantly terrestrial. Thornton (1957) found a rich fauna of arachnids and insects in the swamps of the upper White Nile. He also studied the succession of the fauna as the umbels developed. From closed bud to fully opened umbel, with rays up to 55 cm, took about 40 days. Many of the insects and spiders occurred as solitary individuals, probably using the umbels merely as a substratum to move about on above the water, but there were some species that occurred regularly in considerable numbers.

The sap-sucking Thysanoptera and Homoptera were among the earliest colonisers of the umbels. Figure 2 shows the occurrence of two species of thrips as the umbels age and eventually shrivel. *Catina papyri* was described from Thornton's material, but *Haplothrips avenae* is more widespread; originally found on oats in Malawi. Some species of *Haplothrips* are known to be predators, so it is possible that the later occurrence of *H. avenae* was related to its invasion of the umbels after the development of suitable populations of smaller prey species.

The Homoptera were also early invaders, and the most abundant species was *Schizaphis cyperi*. Among the Heteroptera *Agramma lineatum* was the most frequent, but invaded the umbels somewhat later than the thrips and aphids. Spiders were the latest invaders, reaching their peak as the umbels matured. The Salticidae and Thomisidae were the most frequent, but most of the specimens were immature, making specific identification difficult. These young spiders represent opportunistic invaders from grasslands behind the swamps, moving in to exploit prey populations that had been developing on the papyrus for several weeks. The papyrus umbels provide a constantly changing habitat, with a diverse arthropod community that changes as prey and predator interact.

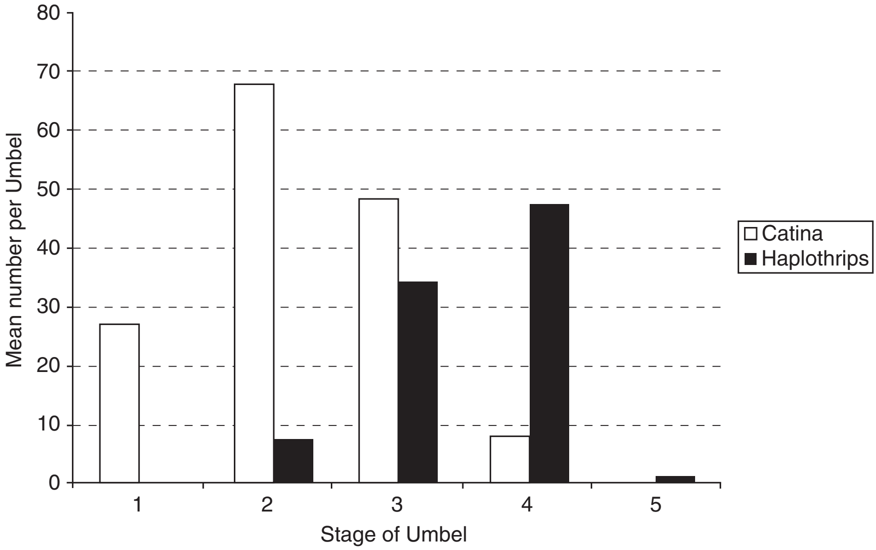

Fig. 2 Succession of two species of thysanopterans on umbels of papyrus; by stage 5, the umbels are dry and shrivelled (based on data given by Thornton, 1957)

9 Fishes

The fishes in the swamps are most diverse and abundant where there are areas of open water. Bailey (1988) has summarised the work of Hickley and Bailey (1986, 1987a, b). In a survey that included a large number of samples from river channels, lakes, shaded swamps and river floodplains they found a total of 68 species, of which 61 were found in the lakes. Each of the other habitats had between 16 and 24 fish species, which were essentially sub-sets of the species found in the lakes. The exception was the killifish *Nothobranchius virgatus*, which was found only in seasonal water bodies at the edges of river flooded grassland, where it fed on micro-crustaceans and insects. *Nothobranchius* has the ability to produce drought resistant eggs, enabling it to survive through the dry season. The lungfish *Protopterus* also occurs in these marginal habitats, but is by no means restricted to them, as it is also found in the permanent shaded swamps. The lungfish can aestivate underground in grassland inside a mucous cocoon, and its lung serves a dual purpose, enabling it to breath in water of low oxygen content, and to survive out of water.

Hickley and Bailey (1987b) divide the fishes of the swamps into five major feeding groups:

1. Mud feeders, such as *Heterotis niloticus* and *Labeo niloticus*. It is probable that *Heterotis* sorts the mud to some extent, so that the ingested material contains a high proportion of ostracods and other benthic microinvertebrates.
2. Microherbivores, such as *Oreochromis niloticus* and *Sarotherodon galilaeus*.

3. Macroherbivores, such as *Distichodus rostrata* and *Alestes macrolepidotus*.
4. Omnivores, eating both plants and animals. The animals may be planktonic, as in the diet of *Alestes dentex*, or benthic as taken by *Synodontis frontosus*.
5. Carnivores. More species fall into this category than any other, and the group can be subdivided in:

   (a) Surface feeders: the best example is the little cyprinid *Chelaethiops bibae*, which feeds entirely on terrestrial insects.
   (b) Zooplanktivores: many juvenile fishes fall into this category, and some adults, such as *Alestes nurse*, take a high proportion of zooplankton, but also include some plant material so that they become omnivores.
   (c) Benthic feeders, such as *Synodontis schall*, taking a high proportion of molluscs, and *Mormyrus cashive* feeding mainly on chironomid larvae.
   (d) Browsers among vegetation, such as *Polypterus senegalensis* and *Micralestes acutidens*, with insects forming a large part of the diet.
   (e) Macropredators such as *Hydrocynus forskalii*, which was found to have eaten 13 species of fish, and *Clarias gariepinus*, which had eaten 12 fish species. Seven other species were macropredators, including *Lates niloticus*, which is the top predatory fish, reaching the largest size and liable only to predation by crocodiles and man.

10 Other Vertebrates

As far as is known there are no endemic amphibians or reptiles in the Sudd, and the roles played there by the various species have not been studied, but have been studied in other localities, for example the detailed study by Cott (1961) of the Nile Crocodile in Uganda. The mammals of the Sudd show varying degrees of adaptation to swamp conditions. The Hippopotamus, well known for its habit of emerging from the water to graze on land at night in other parts of Africa, often feeds during the day while remaining in the water, and consumes plants such as *Najas* and *Vossia*.

Various antelopes occur in and around the Sudd: three examples will suffice to show how they vary in their relationship to swamp conditions. The Sitatunga (*Tragelaphus spekei*) is the most aquatic of the antelopes, with long, splayed hooves adapted for walking in swamps. It feeds in the permanent swamps, and does not make any major migrations. *Kobus megaceros*, the Nile (or Mrs Grey's) Lechwe, is endemic to the Sudd, the Machar Marshes and some tributaries of the Sobat, and makes local movements related to the flood cycle. In general it does not live in the permanent swamps, but follows the waterline of the river flooded grasslands, often wading in shallow water and feeding mainly on grasses. Further away from the permanent swamp the White-eared Kob (*Kobus kob leucotis*) makes long seasonal migrations over hundreds of kilometers, from wet season quarters in southern grasslands east of Bor and Juba to spend the dry season near the River Sobat. The Kob feeds in the grasslands, mainly on *Hyparrhenia* and associated grasses.

Many other herbivores, well known from the African plains, occur on the margins of the Sudd. Elephants make local movements into the wetlands as the water recedes, and even giraffes have been seen wading about in water. Carnivores in the swamps have been little studied, because they are so difficult to see; but the Marsh Mongoose, *Atilax paludinosus*, is seen occasionally, and is probably quite common. It will eat almost anything it can catch, including fish, such as *Protopterus* and *Clarias*, as well as crabs and mussels.

The birds associated with the swamps are dealt with elsewhere (Green, this volume), but the shoebill *Balaeniceps rex* merits special mention in relation to the Sudd, because its lifestyle is linked strongly to aspects of swamp ecology (Fig. 3). The shoebill avoids the main channels and very tall vegetation, preferring smaller channels and pools, frequently surrounded by *Typha*. Much of its diet consists of the air-breathing fishes *Protopterus*, *Polypterus* and *Clarias*, which often predominate when oxygen is deficient in the water. The fish are not stalked, but are ambushed by

Fig. 3 The shoebill (*Balaeniceps rex*), a typical inhabitant of the Sudd and other White Nile swamps and marshes (photograph kindly made available by Pat Morris)

a bird that has been standing motionless beside the water, waiting for a fish to surface for a gulp of air. When the shoebill strikes, its whole body falls forward in an all or nothing attempt to scoop up the fish in its enormous bill. There is no possibility of an immediate second strike if the fish is missed. The nest is usually built on a platform of floating vegetation (Guillet, 1978), and in hot weather the hatched young are kept cool by the parents bringing water back in their bills and showering it over the chicks. In 1978, Guillet estimated the total population to be about 1,500, but in 1983 Mefit-Babtie produced an estimate of 6,000, based on an aerial survey of the Jonglei area alone. The total population of shoebill in the Sudd must be higher than this estimate because it did not include the swamps along the Bahr el Ghazal, where the species is most easily seen through the reduced papyrus fringe. It is possible that the shoebill population was favoured by the expansion of the permanent swamps following the exceptional rains of the early 1960s. No other large bird has its lifestyle so closely linked to the ecology of the swamp, and if a single species can serve as an icon of the Sudd, then the shoebill must be a prime candidate.

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