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Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius* L.) in the Okavango Delta, Botswana

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Summary

The Okavango Delta is a large wetland system situated in northern Botswana. The hippopotamus forms an integral part of this dynamic ecosystem, as it exerts a catalytic effect on geomorphological change. In the distal reaches of the wetland, regular movement of hippos to feeding grounds results in the development of incised channels, which are kept clear of vegetation and act as nodes for swamp expansion. Hippos maintain pathways in backswamp areas, which lead to the development of new channel systems during channel avulsion. They create breaches in the vegetation levees which flank channels in the permanent swamps, causing diversion of water and sediment to backswamp areas. Their paths often lead to lakes in the permanent swamps. During channel avulsion, diversion of a channel into lakes may occur via these paths, which can result in lake closure.

Key words: fluvial geomorphology, hippopotamus, Okavango Delta, wetland

Résumé

Le delta de l'Okavango est un vaste système de zone humide situé au nord du Botswana. L'hippopotame fait partie intégrante de cet écosystème dynamique car il a un effet catalytique sur les changements géomorphologiques. Aux extrémités de la zone humide, les déplacements réguliers des hippos vers les lieux de nourrissage aboutissent au développement de canaux découpés qui sont gardés sans végétation et agissent comme des bourgeons d'extension des marais. Les hippos maintiennent aussi des sentiers dans les parties arrière des marécages, ce qui amène la formation de nouveaux canaux lorsque l'eau est abondante. Ils créent des ouvertures dans les remblais végétaux qui flanquent les canaux dans les marais permanents, provoquant ainsi des déviations d'eau et de sédiments vers les parties arrière des marais. Leurs sentiers conduisent souvent à des lacs dans les marais permanents. Quand les canaux se remplissent, la diversion d'un canal vers les lacs peut passer par ces sentiers, ce qui peut aboutir à la fermeture d'un lac.

Introduction

Numerous studies of the physical and biological impacts which the hippopotamus has on its environment have been undertaken, especially in lake and riverine settings (Pienaar, van Wyk & Fairall, 1966; Thornton, 1971; Lock, 1972;

Eltringham, 1974; Olivier & Laurie, 1974; O'Connor & Campbell, 1986). However, its status in swamp environments is poorly known, especially in the Okavango Delta.

Patterson (1976) noted that although hippos occur throughout the Delta, habitat suited to these animals was under-utilized. He suggested that this may be due to previous hunting both by indigenous people and by crocodile hunters, who used their meat as bait. Stigand (1923) reported encountering numerous and very aggressive hippos in the Nqoga and Maunachira channels during the early part of this century, and speculated that 'four fifths of the hippos of Ngamiland' resided in these channels and the associated lakes. Today, these areas contain relatively few hippos, perhaps substantiating Patterson's (1976) observations. Skinner & Smithers (1990) noted the importance of hippos in keeping channels in the Okavango Delta open, as did Tinley (1966), who specifically mentioned the channels of the more distal swamps. The indigenous peoples of the Delta also recognized their importance, and ascribed the origin of the Nqoga channel and its associated lakes to the actions of hippos (Stigand, 1923). However, to our knowledge, no systematic study of the environmental impact of hippos has been undertaken in the Delta, no doubt because of the immense logistical difficulties involved.

During the course of 10 years of research on the fluvial and vegetation dynamics of the Okavango Delta, we have noted numerous instances where the role of hippos appears to have been pivotal in determining the ecosystem's response to changing conditions, and in this article we compile these observations to emphasize the importance of the hippopotamus in this remarkable ecosystem.

Pertinent characteristics of the hippopotamus

There are several characteristics of the hippopotamus which result in the animal having a significant environmental impact. These are:

(i) the adult is large, weighing between 1000 and 1500 kg (Marshall & Sayer, 1987; Pienaar *et al.*, 1966);

(ii) it is primarily a grazing animal (Mackie, 1976; Lock, 1962; Pienaar *et al.*, 1966), and prefers short grass (<15 cm long; Lock, 1962), preferably previously grazed; it maintains 'hippo lawns' (Olivier & Laurie, 1974) due to its regular grazing of selected areas; and an adult hippo eats about 18 kg of grass (dry weight) per day (Lock, 1962);

(iii) hippos seldom travel more than 2–3 km from water to feed (O'Connor & Campbell, 1986; Lock, 1962);

(iv) while it grazes on land at night, it spends daylight hours in water, preferably sufficiently deep to enable complete submersion, although it also inhabits shallower water where it can 'raft' (Olivier & Laurie, 1974); day living space is sufficiently important that it may be a limiting factor on population numbers (Olivier & Laurie, 1974); moreover, backwaters, rather than flowing water are generally preferred for day living space (Olivier & Laurie, 1974);

(v) hippos use the same paths repeatedly to access their grazing areas (Lock, 1972); and

(vi) the animal is typically gregarious.

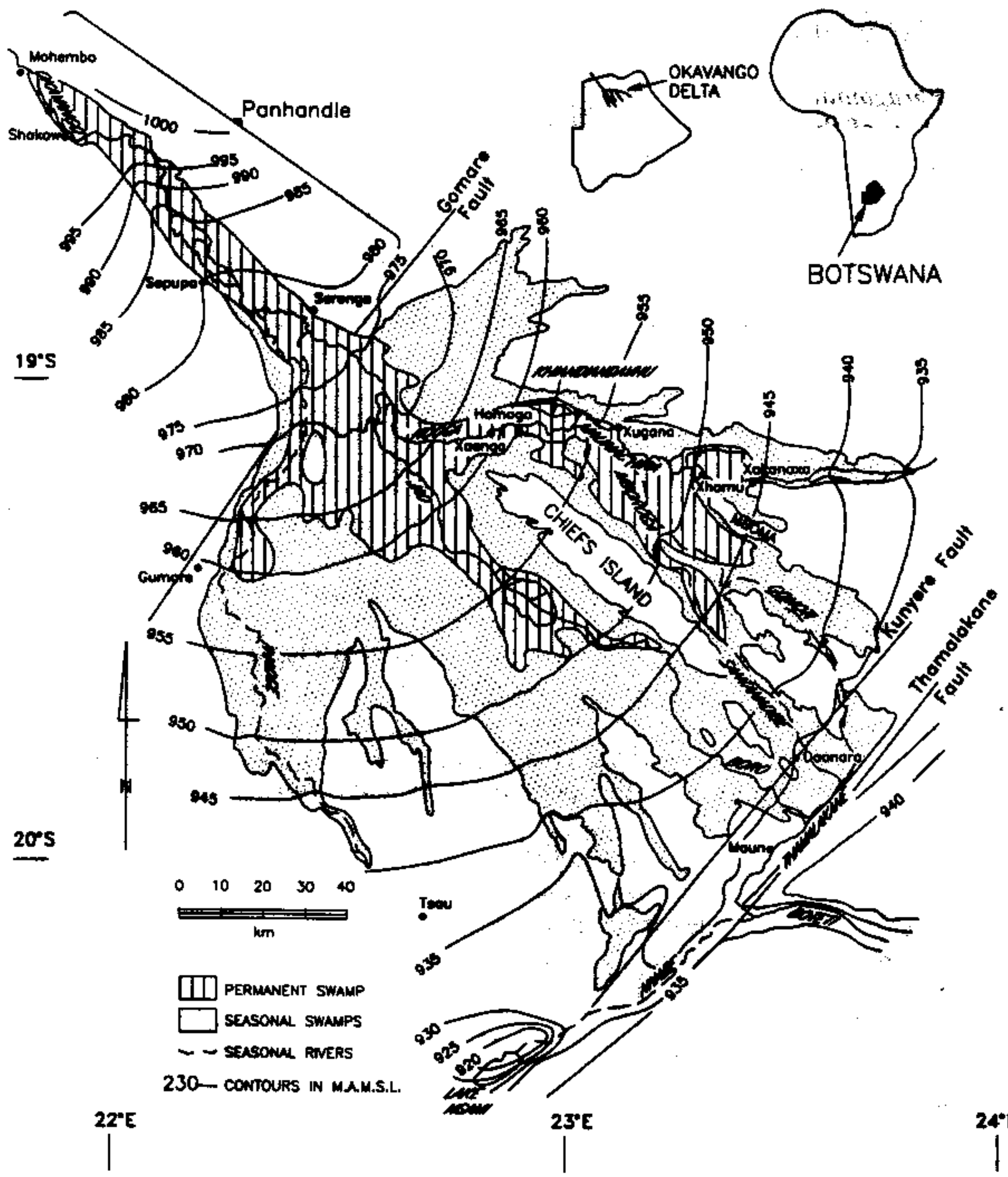

Fig. 1. The Okavango Delta of northern Botswana.

The physical environment of the Okavango Delta

The Okavango Delta is a large alluvial fan which has developed in a rift graben, an extension of the East African Rift system (McCarthy, Green & Franey, 1993a). It is a self-regulating, alluvial depositional system and maintains a regional topographic gradient of 1:3300 (McCarthy *et al.*, in press). It can be divided into several, discrete sub-environments.

(i) The Panhandle region (Fig. 1), a subsidiary graben developed at the apex of the alluvial fan, is characterized by wide channels (50–100 m), typically 3–4 m deep, with a flow velocity between 0·6 and 0·8 ms^{-1}. Channels have sandy beds and are flanked by dense stands of *Cyperus papyrus* (L.) and

Phragamites australis (Cav.) Steud., rooted in mud-rich peat. The flood plain of the Panhandle is flanked by banks of semi-consolidated Kalahari sediment. At the southern end of the Panhandle, the swamp broadens out as it crosses the Gomare fault, forming the alluvial fan.

(ii) The permanent swamps are developed in the more proximal reaches of the fan, with branches extending along major distributary channels (Fig. 1). The north-eastern region of the permanent swamps is served by the Nqoga and Maunachira channels (typically 15–50 m wide and 2–4 m deep). The channels have sandy beds and the margins are densely vegetated by papyrus or *Miscanthus junceus* (Stapf) Pilg., which form vegetation levees (McCarthy *et al.*, 1988; Stanistreet, Cairncross & McCarthy, 1993). Backswamp areas behind these levees tend to be more open and are colonized by a variety of aquatic species (Ellery *et al.*, 1990). Large lakes occur in this region of permanent swamp, representing ancient oxbows (McCarthy, Ellery & Stanistreet, 1993b). Overspill from this region of the swamp supplies the Mboroga– Santantidibe system to the east of Chief's Island (Fig. 1). The swamps in the central region of the Delta have a comparatively poorly developed channel system (Jao-Boro channel) and channel widths are generally less than 15 m. Extensively flooded areas characterize this region (Xo flats).

(iii) The seasonal swamps (Fig. 1) occupy the distal portion of the fan and receive overspill from the permanent swamps during the advance of seasonal flood waters.

(iv) Islands occur throughout the Delta, but become more frequent down the fan. They vary in size from individual anthills to Chief's Island, a large tectonic uplift in the central portion of the Delta. Trees are confined to the islands, and vegetation on these islands is typically zoned (Ellery, Ellery &McCarthy, 1993a), with broad leaved evergreens occurring around the island margins, deciduous trees and palms forming successively inner rings and grassland dominating the island interior. Groundwater beneath the islands is frequently saline (McCarthy, Ellery & Ellery, 1993c), which inhibits vegetation growth on the interior of islands.

The local scale topography of the fan surface is gently undulating, with relief seldom exceeding 1·5 m. Termitaria form the highest topographic features. This gently undulating topography is responsible for the numerous islands. Water throughout the Delta is exceptionally clear (turbidity less than 10 NTU) due to the very low suspended sediment load in the Okavango River (McCarthy, Stanistreet & Cairncross, 1991).

The impact of the hippopotamus

Hippos require permanent, deep water for day living space and hence their primary habitat is the permanent swamp. However, their limited feeding range results in severe local overgrazing, so that in years of good floods, they extend their range and may take up residence in the seasonal swamps. Provided there is sufficient water available for day living space, it is not uncommon to find hippos resident as far south as the Thamalakane River, even within the municipal

Fig. 2. A 'hippo lawn' on an island in the swamps. Regular grazing by hippos keeps the grass short.

boundaries of the town of Maun, where they share grazing with donkeys and other domestic stock.

The present status and distribution of hippos in the Okavango is not known, and the most recently published study is that of Patterson (1976). Their impact on the environment is, however, abundantly evident. Unlike the situation in riverine environments, the major impact of hippos in the swamp environments of the Okavango arises from their trails.

Most hippos reside in the permanent swamp. Suitable grazing is generally to be found on islands, where 'hippo lawns' (Fig. 2) are commonly encountered. The gently undulating topography of the swamps means that deep water, suitable for day living space, is generally located some distance from islands. Consequently, hippos establish a network of trails through the swamps which link lakes, channels and islands. The trails made by hippos are different from those made by terrestrial species such as elephant (*Loxodonta africana* (Blumenbach)) or buffalo (*Syncerus caffer* (Sparrman)). These trails cross water from island to island (Fig. 3), whereas hippos tend to establish trunk paths which are aligned with the prevailing slope, albeit rather sinuously, and follow the lower ground, hence remaining in water. Lateral trails branch to islands from these trunk paths. The geomorphological consequences of these trails varies, depending on their location.

(i) Trails on the fringes of the permanent swamp

The regular movement of hippos along trunk trails keeps them clear of vegetation, and as they are often orientated down the regional topographic gradient, there is more pronounced flow along these channels. Flow, coupled with the disturbance generated by the regular movement of hippos, especially entire pods, leads to erosion of the sandy substratum. Over time, these paths enlarge and become incised, and paths in excess of 1m deep and 2 m wide are common. Such paths are particularly evident on the fringes of the permanent swamps, especially in the north-eastern region, and good examples occur north of Mboma Island (Fig. 1). These are used by hippos travelling between lakes

Fig. 3. Animal (mainly elephant) trails crossing an area of swamp from an island in the foreground to another in the centre of the photograph. Several hippo trails are also developed in the swamp and run across the photograph from left to right, crossing the elephant trails at right angles.

such as Xhamu and the Mboma mainland. Channel encroaching species, notably *Ficus verruculosa* (Warb.), commonly occur in these areas (Smith, 1976; Wilson, 1973) and it is only the regular movement of hippos that prevents complete vegetative closure. It is undoubtedly this phenomenon that Tinley (1966) observed in his survey of the Moremi Game Reserve. We have observed that elephants also occasionally use these channels as pathways, although the reason for this is not clear. The larger trails created in this way have a pronounced vegetation fringe, and hence can be seen on high resolution satellite imagery, where they appear as long, sinuous ribbons and networks, extending out from, and connecting, inundated areas (Fig. 4).

The distribution of water across the Delta is constantly changing (Ellery & McCarthy, 1994). When an increase in discharge occurs to a new area of swamp, it is likely that these distal, incised, hippo trails become new channel systems. This appears to have been the case when the Nqoga channel assumed ascendance over the failing Thaoge (Stigand, 1923). The Boro channel possibly originated in a similar way. Because hippo trails on the fringes of the swamps are often orientated down the regional slope, and are therefore exploited by flowing water, they are of far greater importance to geomorpholocial change than the trails of any other species.

(ii) Access trails to islands

Islands are the primary feeding sites of hippos in the interior of the swamps, but are usually small (a few hectares), and grass cover is limited by the trees. Consequently, access trails to islands are generally less frequently travelled, and moreover, have no flow. They are therefore less well developed than trunk trails. Islands, especially those in the permanent swamps, become affected by the accumulation of saline ground water beneath their surface, which impacts catastrophically on island vegetation (Ellery *et al.*, 1993a). Over time (perhaps one to two centuries), all vegetation on such islands is destroyed and they cease

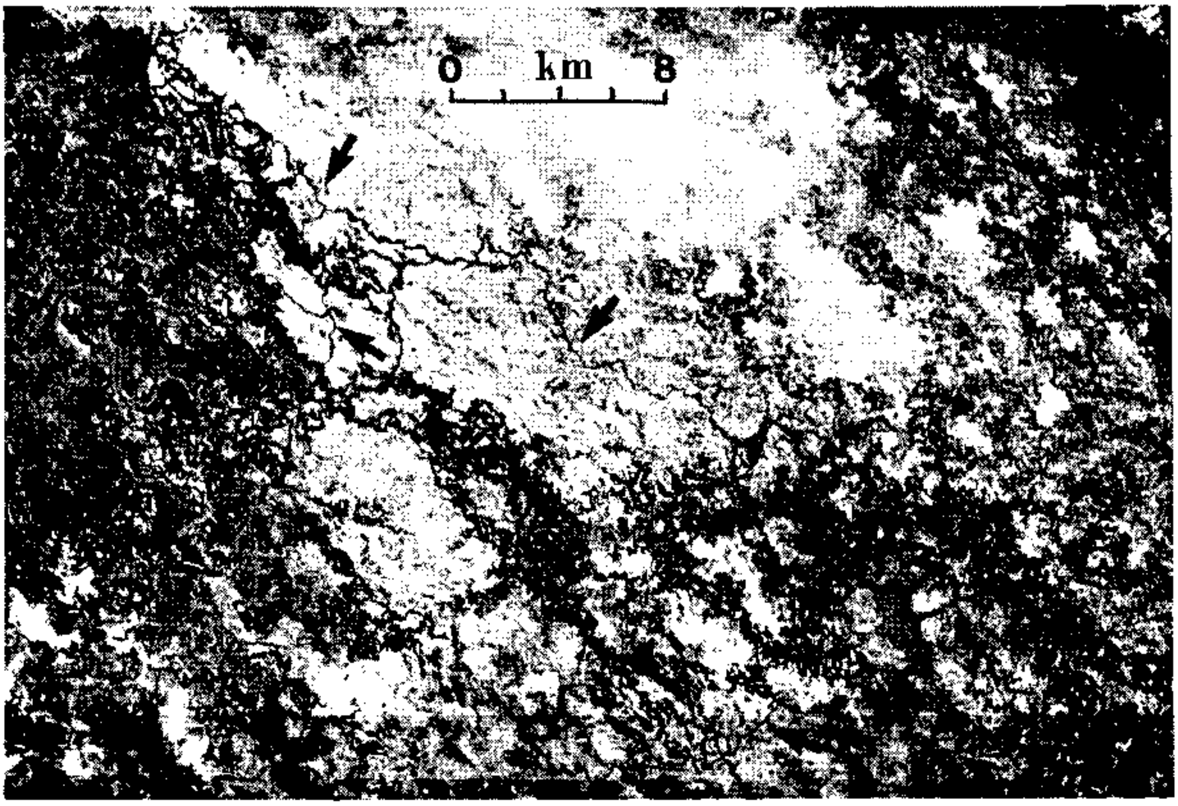

Fig. 4. LANDSAT TM image of an area in the north-eastern swamps, showing sinuous trails made by hippos (arrowed).

to be visited by hippos. Swamp vegetation overgrows the access paths, and because hippos defaecate in water (Olivier & Laurie, 1974), it appears that these pathways become areas of nutrient enrichment, as abandoned hippo trails are invariably marked by a line of more luxuriant vegetation.

(iii) Trails in lakes

Hippos do not only maintain pathways in swampy terrain. In the large lakes of the permanent swamp, where hippos often spend daylight hours, the resident hippo pod is invariably to be found in the same small area of the lake. They maintain a network of paths across the lake bed from this domicile area, leading to access channels and to local islands. These trails can frequently be seen from the air, the sandy trail being visible as a yellow ribbon across the lake bed. Figure 5 shows such a trail on the bed of a dry lake in the Daonara area. The trail is incised due to frequent use and indicates that the regular passage of hippos has an erosive effect, even in the absence of flow. The reason that hippos restrict their movements to these paths may be due to the fact that lake beds are sites of accumulation of fine organic detritus which may attain a thickness of more than two metres (McCarthy *et al.*, 1993b) and, in addition, support the growth of various submerged aquatic species. Straying from the pathways would therefore reduce visibility for the hippos and their movement would be impeded by the vegetation.

(iv) The effect of hippos during channel abandonment

Hippos make use of the major distributary channels of the Delta for travelling purposes. These channels enable the discharge of sandy bedload sediment.

Fig. 5. A hippo trail on the bed of a dry lake in the Daonara area.

Because the channel margins consist of vegetation rooted in peat, they are permeable and consequently, water is continually leaking from the channels. As a result, the ability of a channel to transport bedload declines downstream, and bedload is deposited along the channel bed, causing vertical aggradation of the channel. Water loss from the channel is enhanced, which in turn promotes growth of the flanking vegetation. This process causes the water level in the channel to become elevated relative to the backswamp areas (McCarthy, Ellery & Stanistreet, 1992). The process of vertical aggradation ultimately destroys a channel, because, as down-channel gradient declines, flow becomes slower, and the channel becomes overgrown with aquatic plants. Water diverts elsewhere and eventually the channel and flanking swamp desiccate. Fires destroy the accumulated peat (Ellery *et al.*, 1989) and the entire affected area of swamp reverts to dry land or seasonal swamp.

Hippos continue to utilize channels during their decline. Vegetation encroaches from the channel margins, but hippos maintain a clear pathway along the old channel course (Fig. 6). This undoubtedly prolongs channel life, but is insufficient to maintain the channel. Net aggradation renders the channel hydraulically unfavourable and water diverts elsewhere, so that the channel ultimately fails. Such a fate befell the Thaoge channel along the western side of the Delta. Evidence for the continued use of the channel by hippos during its failing stage was found in excavations in the bed of the old Thaoge channel at Tsau (Fig. 7). The white sand (A in Fig. 7) was deposited during the active stage of the channel and contains large (20–30 cm) bedforms. As the channel began to fail, flow velocities declined and plants began to encroach on the channel, so that organic matter with entrapped mud began to accumulate along with bedload

Fig. 6. A hippo trail along the failing Nqoga channel.

Fig. 7. Sedimented hippo trail in the bed of the abandoned Thaoge river, at Tsau. See text for details.

sand (B in Fig. 7). Hippos created a discrete channel during this stage, which initially became deeply incised into the older channel sediment (C in Fig. 7). This incised trail gradually became filled with a mixture of sand and muddy organic material as the channel continued to fail. Eventually, hippos abandoned the area completely, and the entire area became vegetated, so that the former hippo trail and the flanking areas were draped with a layer of mud (D in Fig. 7), the residue from the burning of peat which formed during the final stages of channel failure.

(v) Trails connected to major channels

Hippos maintain narrow side channels through the vegetation levees which flank major channels, to obtain access to backswamp areas, lakes and islands. During the aggrading stage of a major distributary channel, lateral water surface gradients may increase to become steeper than the down-channel gradients (Stanistreet *et al.*, 1993). Water then discharges rapidly down hippo trails leading

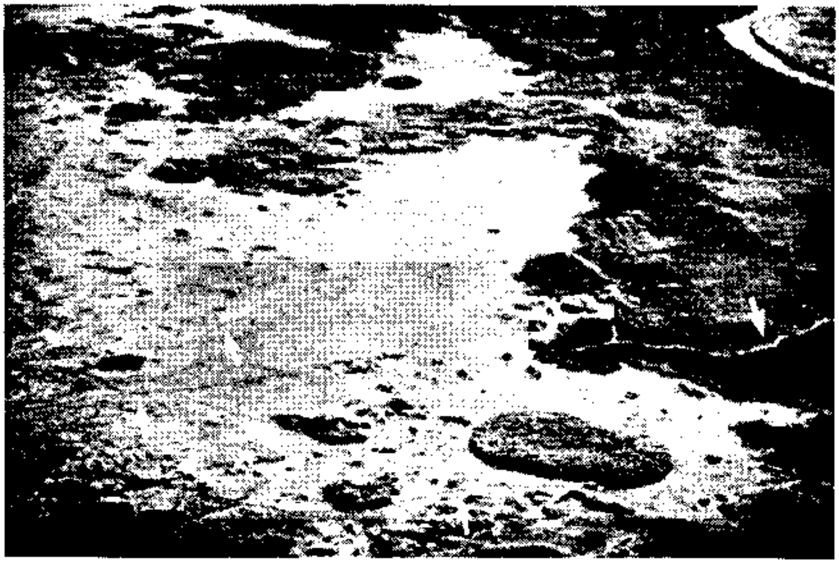

Fig. 8. Small sand delta (white) at the entrance to a hippo trail leading from a sparsely vegetated backswamp area to an aggrading channel (top right). The backswamp area is transected by a maze of hippo trails (arrowed).

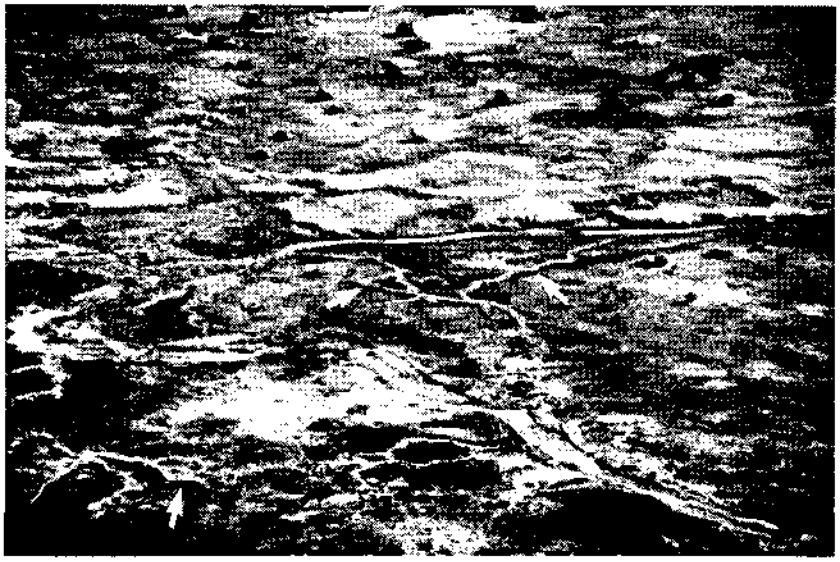

Fig. 9. Former hippo trails (arrowed) forming sandy ridges along the abandoned Nqoga channel.

from such a channel, transporting bedload along with it (Fig. 8). The beds of these hippo trails aggrade as the main channel aggrades, and when the channel system finally fails, is abandoned, and the accumulated peat has burnt off, the former hippo trails stand out as sinuous, sandy ridges, sometimes more than a metre high (Fig. 9; Stanistreet *et al.*, 1993). These ridges may later create areas suitable for the formation of islands.

Occasionally, a hippo trail leading from an aggrading channel discharges directly into a lake, which hippos use as day living space. A well documented instance of such an occurrence is that of Bokoro lake, which lay close to the aggrading Nqoga channel. As the Nqoga channel aggraded and failed from its distal end, an increasing quantity of water was diverted into the hippo trail which became widened by erosion. The influx of sediment and nutrient-rich water caused

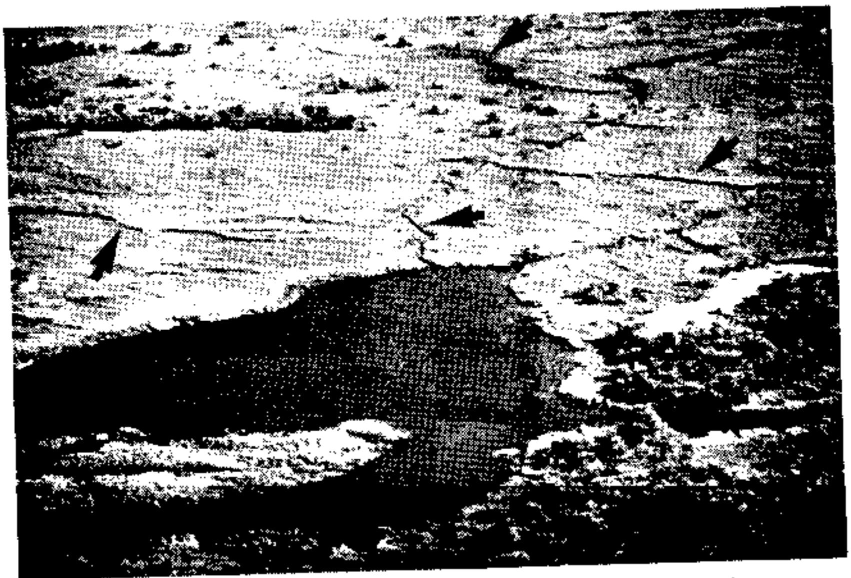

Fig. 10. A network of hippo trails (arrowed) in densely vegetated swamp surrounding a small lake.

rapid filling of Bokoro lake and it disappeared in a few decades (McCarthy *et al.*, 1992). The infilling of Dxherega lake, which is currently taking place, is also partly a consequence of this diversion (McCarthy *et al.*, 1993b). Indeed, the diversion of major channels into lakes and their subsequent infilling by sediment and peat is primarily due to the action of hippos, whose trails link lakes to major channels. Isolated lakes, in contrast, tend to be stable over many decades.

(vi) Trails in backswamp areas as sites for new channel systems

Hippos maintain a network of channels in backswamp areas (Figs 8, 10). In these areas, there is invariably a thick accumulation of organic debris (Ellery *et al.*, 1990) and many of the trails are therefore well utilized. This network of trails is particularly important in swamp hydrology. During the period of rapid aggradation which precedes channel failure, water discharges strongly through the channel margins into backswamp areas, leading to an increase in flow through these areas. The network of hippo trails which have developed there provide low resistance flow paths, and hippo trails orientated in the most favourable direction with respect to the local hydraulic gradient experience an increase in discharge. Erosive widening and deepening of these hippo trails occurs and they ultimately develop into a new channel system which flows sub-parallel to and overlaps the failing channel. These overlap regions were recognized by Wilson (1973), who termed them 'filter areas'. The new channel system propagates upstream as the major channel system fails (McCarthy *et al.*, 1992). The sinuosity of the resulting new channel is thus inherited from the previous network of hippo trails. The Maunachira channel probably developed in this way as the Nqoga failed (Ellery *et al.*, 1993b). The Khiandiandavhu channel is an embryonic channel system developing along a network of hippo trails, also related to the failure of the Nqoga channel (McCarthy *et al.*, 1992).

(vii) Hippo trails in the Panhandle

Hippos are fairly common in the channels in this region, but islands are few in number, so grazing areas occur only along the edges of the floodplain, generally some distance from the channels. Hippos gain access to grazing areas by way of channels leading either directly from the main channel system or via channels leading from side embayments to the main channels. The sedimentary processes operating in the Panhandle are different from those on the fan (McCarthy, Stanistreet & Cairncross, 1991). The Panhandle channel is actively meandering, and large point bars are common features. Migration of meanders leads to the formation of an alluvial ridge, with the river system occupying an elevated position relative to its distal flood plain (Smith *et al.*, 1989). A breach in the channel margin may divert the river into the backswamp areas, where a new meander system will, in time, develop. This process of avulsion is currently taking place in the Panhandle (Smith *et al.*, in press). The initial avulsion appears to have been induced by neo-tectonic activity, but secondary avulsive channels have developed along former hippo trails (Smith *et al.*, in press).

Conclusion

The Okavango Delta is an aggrading alluvial system. It maintains a very low regional gradient (1:3300), which is a consequence of the interaction of a multiplicity of factors, including clastic sediment load, solute load, climate, vegetation and earth movements. The dispersal of water is a key factor in regulating the gradient, as water is the transport medium of the sediment, and moreover, sustains the vegetation. Hippos are an integral part of this dynamic system, and they exert a catalytic effect on changes within the system. As a result of their regular habits, they create more favourable routes for water dispersal, thereby initiating a variety of fluvial and sedimentary phenomena, including entirely new channel systems, and the infilling of lakes. On a local scale, they maintain minor channels. Their role is limited by regional factors. If the regional gradient is favourable, their regular movement keeps channels open or creates new channels. However, if the regional gradient is unfavourable, their influence on the fate of a channel is minimal.

The hippopotamus is an important component of the Okavango ecosystem whose influence is far greater than that of any other mammalian species. There can be no doubt that without hippos, the characteristics of the fluvial system on the fan would be different. The conservation of hippos is therefore essential and moreover, detailed study of the hippos in the Okavango is overdue.

Dedication

This paper is dedicated to the memory of Struan Charles Andrews, who died tragically while pursuing his dream of studying hippos in the Okavango.

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