Abstract — Current knowledge of pans, rivers and artificial waterholes in the three adjoining protected areas of the south-western Kalahari is synthesized and their ecological components are examined in relation to the overall Kalahari ecosystem. Although the pans and rivers are normally dry they have many features not found in the sandveld, and so form important subsystems in the overall ecosystem. The main difference between the pan and river ecosystems is their drainage, which is endorheic and open respectively. This difference necessitates different conservation strategies for the two systems. Self-maintenance and self-regulation in the pan ecosystem is discussed and it is shown how the combined interactions of the biotic and abiotic components are essential for these processes. Artificial waterholes are not an essential source of moisture for Kalahari fauna but may play a role in stabilizing or concentrating certain populations. When waterholes are highly mineralized they also provide an additional source of minerals for the fauna. The ecological significance of pans, rivers and artificial waterholes in the Kalahari ecosystem needs further investigation.

Introduction
This paper aims at synthesizing current knowledge of pans, rivers and artificial waterholes in the three adjoining protected areas in the south-western Kalahari. These areas are the Kalahari Gemsbok National Park in the Republic of South Africa, and the Gemsbok National Park and the Mabua Sehube Game Reserve in Botswana (Fig. 1).

The geology, soils, vegetation and fauna of the area are discussed by various authors in this special edition and in this paper the pans, rivers and artificial waterholes will be examined in relation to the overall Kalahari ecosystem.

The climate of the area is characterized by low annual rainfall (250 mm or less) with a high co-efficient of variation and the rain often falls as short-duration, high-intensity thundershowers. The relative humidity is low and the annual evaporation rate is high. Summer air temperature is high although, in winter, it often falls to below freezing at night. The winds are most frequent and violent at the end of the dry season in August and September.
Fig. 1. Pans, rivers and artificial waterholes in the protected areas of the south-western Kalahari.
The most striking feature of the geology is the almost uninterrupted mantle of sand covering the area. Underlying this sand mantle are calcareous and silicified sand and sandstone, grit and minor conglomerates, which form a tableland of varying thickness below the sand mantle. The sand mantle is between 3.5 m and 35 m thick and is unbroken except at pans and rivers (Boocock & Van Straaten 1962). Underlying the surface of the pans is a series of clays, marls and carbonates which appear to have been laid down under shallow lacustrine conditions which fluctuated over a period of time (Lancaster 1974).

The soils of the dunes and undulating flats contain everywhere a sand fraction (2.0 – 0.02 mm diameter) of > 95%, and are either red or pink in colour with red by far the commonest. The colour is due to a coating of ferric oxide around the particles. No distinct horizons occur in these sandy soils, and the sands, both red and pink, are poor in nutrients (Leistner 1967). Only in deep dune valleys are the pink sands somewhat richer in water-soluble Ca, due to the calcrete layer being near the surface.

The vegetation is mainly an open to very open tree or shrub savanna with dwarf-shrub and grass formations associated with pans and rivers (Werger 1978).

Results

Pans

There are numerous pans in the three adjoining protected areas (Fig. 1). These pans do not occur evenly throughout the area, nor do they appear to have any characteristic size, shape or pattern, apart from a slight linear arrangement in the north-western part of the Gemsbok National Park. Similar pans are found throughout the Kalahari (Parris 1976). Leistner (1967) reports that pans in the southern Kalahari duneveld are usually found associated with flat ground that has little or no overall surface gradient and that the main concentration is found in the south-western sector between Aroab, the confluence of the Nossob and Molopo Rivers, and Upington. In the Central Kalahari, Parris (1976) found no consistent pattern in the distribution and arrangement of pans although there are noticeably more pans in the central area, roughly coinciding with the Bakalahari Schwelle or Rise, which forms the ancient watershed between the north and east flowing Okwa River and the south and west flowing Nossob and Molopo Rivers. In some areas, particularly near dry riverbeds, the pans are arranged in lines which coincide with old tributaries of the dry rivers.

Leistner (1967) describes pans in the southern Kalahari as generally flat-bottomed depressions periodically containing water and classifies them into various groups, the most common type being the kalkpan or calc-pan. A less common type of pan in the southern Kalahari has a high concentration of minerals, mainly Na and Cl, on its floor and is referred to as a salt-pan. Rarest in the southern Kalahari are rock-pans, which occupy depressions in seemingly solid bedrock, while shallow depressions lined with compact calcareous sand and situated on sandy flats or between ridges are known as sand- or dune-pans.
Leistner (op. cit.) notes that one feature which is characteristic of virtually all large pans in the southern Kalahari is an accumulation of sand on the lee side (which is almost invariably the south-east) of the pan. These dunes are normally higher and always lighter in colour than others in the vicinity. Blair-Rains & Yalala (1972) describe pans in the central Kalahari as flat-floored depressions of variable size, lying 15 m or more below the surrounding surface, which frequently have a pronounced tree- or shrub-covered ridge (lunate dune) along their south or southwestern edge. Lancaster (1974) describes how two dunes can be identified at pans but they may merge into one in a few cases. He reports that the dune area consists of a larger, outer dune, and a smaller, inner dune. Both dunes are crescentic or parabolic in form with their main bulk opposite the centre of the pan and their “horns” curving part way around the pan depression. The dimensions of the pan dune and pan floor vary considerably. On some pans the pan dune is scarcely noticeable while on others, such as Mabua Sehube, it forms an impressive sandy hill. Similarly the pan floor may be less than 30 m in diameter in the case of small, shallow pans, while the diameter of the pan floor on many of the larger pans exceeds a kilometre.

The physical and chemical properties of pan soils are described by Parris (1976) and their important properties are summarized as follows:

(i) The pan has a wider range of soil types than the sandveld and there is a gradient of both chemical and physical properties of the soils from the centre of the pan outwards towards the rim.

(ii) The soils are generally more compact than sandveld soils but range from hard, almost impenetrable, soils on the pan floor to loose, well-drained soils on the pan dune.

(iii) The soils have a higher mineral content than soils in the sandveld, with the highest mineral concentrations on the pan floor.

A feature of pans in the Kalahari is the presence of one or more salt-licks on the pan floor (Parris & Child 1973) and these salt-licks are characterized by:

(i) Distinct game trails leading directly to the salt-lick, often from a fair distance off the pan.

(ii) A heavily trampled area around the salt-lick.

(iii) One or more local depressions up to a metre deep in the otherwise flat pan floor where the soil has been stripped and eaten away by game.

(iv) Soil with a slightly or very salty taste, often with saline crystals visible in the soil.

All the salt-licks analysed by Parris (1976) were found to have a higher pH, electrical conductivity and total mineral content than the soil immediately adjacent to the salt-lick. However, as far as the individual mineral components were concerned, the various mineral fractions were not all found to be consistently higher in the salt-licks than in the adjacent soil.

Sandveld soils have a low mineral content and salt-licks are restricted to pans and pan-like areas and a few sites in the calcrite cliffs of the Nossob River. Kreulen (1980) discusses how salt-licks may be vital to ungulates in the Kalahari because of their multiple benefits including serving as a source of nutrient minerals and buffering materials.
Because the overlying sand mantle is extremely porous, virtually all the rainfall is immediately absorbed and retained as capillary water by the sand. It is only on pans and rivers that the combination of slope and less porous soils results in a certain amount of surface water accumulation after rain. The calcrite outcrops and banks have holes and cavities in the upper few metres, which fill with water after rain. Because the lower layers are usually impervious, these calcrite outcrops often retain this water just below the surface and where the local topography is suitable, this water drains out onto the pan as a small natural spring. Although the wildlife can survive without surface water (Parris 1971), most species drink at the waterholes when they hold water and nomadic waterbirds are present in the Kalahari only while the waterholes hold water.

Since pans comprise a variety of soil types, they support a relatively wide variety of plant species, many of which are not found in the sandveld. This is reflected in the marked differences found in the grasshopper species recorded on pans and in the sandveld (Barker 1983).

Two characteristic features of the vegetation on pans are its concentric zonation on the pan caused by physical and chemical gradients in the soil and its Karroid nature (Leistner 1967; Parris & Child 1973). Kreulen (1980) showed that grasses growing on pans and rivers are significantly better in nutritional quality than grasses growing in the sandveld and that the dwarf shrubs on the pans may form an important part of the diet of springbok (Antidorcas marsupialis).

Parris (1976) illustrates the general physiognomy of pan vegetation in the dry season (Fig. 2) and gives the average dry season height (Fig. 3) and average dry season ground cover (Fig. 4) of the perennial grasses and woody plants on a cross-section of pans. Almost all parts of the pan (except the pan floor of highly saline pans) were shown to have a reasonably dense ground cover under natural conditions, although the grasses were grazed short towards the centre of the pan.

Smithers (1971) and Parris & Child (1973) reported that many of the wildlife species in the central Kalahari make extensive use of pans. Their activities include feeding on pan vegetation, utilizing salt-licks and seasonal waterholes, and utilizing the compact soils and calcrite banks for their burrow systems. Parris (1976) recorded all the larger mammal species on pans and showed that the majority of the smaller mammals utilized pans. Parris & Child (1973) also showed that the combined density of the common larger antelope, i.e. springbok (Antidorcas marsupialis), red hartebeest (Alcelaphus buselaphus caama), blue wildebeest (Connochaetes taurinus) and gemsbok (Oryx gazella), on pans was from four to 26 times greater than their density in the surrounding sandveld in Mabua Sehube Game Reserve.

When the geomorphology, soils, vegetation and fauna of pans are considered together, then pans are seen to have a number of features not found in the surrounding sandveld. These features are:

(i) Calcareous soil, lying below the general level of sandveld.
(ii) Endorheic drainage.
(iii) An increasing concentration of minerals and clay particles in the soil, from the highest to the lowest part of the pan.
(iv) Salt-licks and seasonal waterholes on the low-lying parts of the pan.
Fig. 2. Diagrammatic cross-section through a typical pan in the Central Kalahari, Botswana, showing the physiognomy of the vegetation during the dry season. The physiognomic types shown on the pan profile indicate the most common types on each section of the pan but overlaps often occur.
Fig. 3. Average dry season height in mm of the perennial grasses and woody plants (shrubs and trees) on and around a cross-section of six pans in the Mabua Sehube and Khutse Game Reserves in the Central Kalahari, Botswana. Plant height was recorded during routine vegetation assessments and the columns below the pan outline are the average of all perennial grass heights and the average of all woody plant heights recorded during the study period (1968 to 1972). Measurements of pan floor vegetation were made on the section with the best perennial grass cover.

Fig. 4. Average percentage ground cover of the perennial grasses and woody plants (shrubs and trees) on and around a cross-section of six pans in the Mabua Sehube and Khutse Game reserves, Central Kalahari, Botswana. Percentage ground cover was recorded during routine vegetation assessments and the columns below the pan outline are the average of all perennial grass cover percentages and all woody plant cover percentages recorded during the study period (1968 to 1972). Measurements of pan floor vegetation were made on the section with the best perennial grass cover.
(v) Concentric bands of relatively short and dense vegetation with many Karroid features and with grasses having a significantly higher nutritional quality than sandveld grasses.

(vi) A relatively high average density of wild animals with a correspondingly high rate of animal activity.

The pans constitute, therefore, a distinct habitat or subsystem within the larger Kalahari ecosystem and as such they enhance the overall Kalahari ecosystem by increasing its spatial heterogeneity and by providing key habitats for many species. Further research on the rôle of these important habitats in the Kalahari system is needed.

Odum (1971) states that ecosystems are capable of self-maintenance and self-regulation and Parris (1976) discusses self-maintenance and self-regulation in the pan ecosystem as follows:

Fig. 5. Diagrammatic representation of soil movement in a pan ecosystem in the Central Kalahari, Botswana. The amount of soil moved by the various factors is small compared with the amount of soil on the pan but is sufficient to maintain the shape of the pan.

Rain in the Kalahari falls mainly in the form of thundershowers during which the amount of rain falling per unit time is high. The shape of the pan, and the fact that the pan soils on the lower banks have a fairly high silt and clay content, result in some of the water being channeled inwards towards the centre of the pan as run-off water (Fig. 5). This results in a higher effective rainfall in the lowerlying parts of the pan, and the run-off water also carries with it particles of soil, particularly the finer particles, organic matter such as plant litter and faunal remains, and soluble soil minerals. In this way soil is moved downwards and inwards towards the centre of the pan and fine soil particles, soil minerals and organic matter are concentrated in the lower parts of the pan, with the lowest part of the pan having the highest concentration.

This concentration of fine particles on the pan floor leads to the formation of temporary open pools and the concentration of minerals leads to the formation of salt-licks.

The higher effective rainfall on the lower parts of the pan, combined with favour-
able physical and chemical properties, enables these soils to support their typical relatively dense and nutritious vegetation.

The relative use of the different parts of the pan by grazers, (*i.e.* gemsbok, red hartebeest and blue wildebeest), browsers and mixed feeders (*i.e.* kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*) and springbok) and springhares (*Pedetes capensis*) and hares (*Lepus* spp.) is given in Fig. 6 and the impact of the combined grazing and trampling pressure of the larger antelope, springhares and hares on pan vegetation is shown to be considerable. A 10 × 10 m plot on the pan bank on Mabua Sehube Pan was protected from large antelope, hares and springhares by means of a thorn bush fence from 1969 to 1972 and after three years, the difference in the dominant perennial grass *Stipagrostis obtusa* between the protected plot and the adjacent unprotected area is illustrated (Fig. 7). The grazing and trampling pressure in the surrounding sandveld is relatively light and there was no observable difference in perennial grass cover between a similar protected plot and the adjacent unprotected area in the sandveld.

![Diagram](image)

**Fig. 6.** Average number of pellet groups per 20 plots 3.8 m² each on and around a cross-section of six pans in the Mabua Sehube and Khutse Game reserves, Central Kalahari, Botswana. Pellet densities of large ungulate grazers (gemsbok, red hartebeest and blue wildebeest), large ungulate browsers and mixed feeders (springbok, kudu and eland) and hares and springhares were recorded during the study period (1968 to 1972). The columns below the pan profile indicate the average of all pellet densities for the study period.

Ground squirrel (*Xerus inauris*) in the central Kalahari are particularly associated with pans (Smithers 1971) and live in colonies of up to 30 individuals on the hard soils on the pan floor or pan edge. They feed up to 200 m from their burrows (*Smithers op. cit.*) and have a considerable impact on the pan vegetation in the immediate vicinity of their burrows. The seven small rodent species found on pans feed on all parts of the pan and on all types of pan vegetation. They are often responsible for extremely heavy local use of pan vegetation and may completely destroy the perennial vegetation in the immediate vicinity of their burrow.
A bush exclosure $10 \, \text{m} \times 10 \, \text{m}$ was erected on a section of pan bank vegetation on Mabua Sehube Pan, Central Kalahari, Botswana, on 6 November 1969. The vegetation inside and outside the exclosure was similar. The exclosure was photographed on 10 July 1972 and photograph (a) shows the vegetation inside the bush exclosure and photograph (b) shows the vegetation outside and adjacent to the bush exclosure.
During the rainy season when the pan vegetation is fairly dense and tall, the soils are moist and firm and wind blowing across the pan has little effect on the pan soils. However, towards the end of the dry season, the vegetation is short and sparse and the soils are dry and heavily trampled and Parris (1976) shows how, under these conditions, the wind does erode a fair amount of pan soil. Since wind erosion in the surrounding sandveld is relatively limited there is a net loss of soil to the pan (Fig. 5). The dunes on the leeward side of most pans are an illustration of the extent of this wind action on pans over time.

The extent to which the salt-licks are used by the larger herbivores is demonstrated by the observation that the main game tracks on a pan invariably lead directly to the salt-licks, and by the heavily trampled appearance of the area around the salt-licks. Antelope eating the salt at these salt-licks is a common sight on pans.

Large carnivores and large herbivores use the waterholes on pans when water is available and the tracks of some of the smaller mammals are often seen around these waterholes. The use of both the waterholes and the salt-licks on the pan results in the removal of soil from the pan floor. In the case of the salt-licks the soil is actually eaten while, in the case of the waterhole, the soil adheres to the animals in the form of mud and is carried away from the pan. Young (1970) illustrated how buffalo in the Kruger National Park enlarge natural waterholes by a combination of trampling, rolling and carrying away the mud which adheres to them and Smithers (1971) refers to the considerable amount of mud carried away by animals from the waterholes on pans in the Kalahari.

Although there is no quantitative data on the amount of soil removed from the pan in this way, what is of particular importance is that, since both the salt-lick and the waterhole lie near the centre of the pan, soil is constantly removed from the deepest part of the pan. This removal of soil increases the depth of the pan floor relative to the pan rim and the surrounding sandveld and so helps maintain its ecologically significant saucer-like shape.

Many of the smaller mammals dig into the soil on the pans in search of food and Smithers (1971) describes some of the smaller carnivores, such as the bat-eared fox (Otacyn megalotis) and the suricate (Suricata suricatta), as avid diggers, digging even in the hardest soil.

- Almost all the smaller mammals living on pans have burrow systems and these burrow systems are a conspicuous feature of pans. They are found from loose sandy soil to the hardest calcrete outcrops and on all sections of the pan. It is only on the bare floors of highly saline pans that burrows are rare or absent.

This extensive digging and burrowing activity on pans results in a continuous turning of the pan soils and is particularly important in breaking up the underlying calcrete and mixing it with the overlying sand. This mixing and consequent exposure to other natural soil-forming agents leads to the development of the characteristic pan soils. It was the apparent paradox of a high rate of soil erosion in a relatively stable ecosystem that first highlighted the importance of soil forming factors in the system.

The pan vegetation plays an important rôle in buffering the rate of soil erosion through its ability to withstand heavy herbivore pressure. The value of this buffering function is illustrated by Parris & Child (1973) who showed that at pans where
the vegetation has been almost destroyed by livestock the rate of soil erosion is increased to the point where the soil is blown into atypical small dunes on the pan and the characteristic shape of the pan is altered.

Although the rôle played by some of the major biotic and abiotic components in maintaining and regulating the pan ecosystem has been illustrated by Parris (1976) further research is needed on the significance of other components such as microclimatic factors, large carnivores and invertebrates in the system.

Rivers

There are two rivers in the protected areas, the Auob and the Nossob. Both rivers rise outside the protected areas, entering from the west, and join up near the southern boundary, where they leave the area as one river (Fig. 1).

Bothma & De Graaff (1973) describe the Auob and Nossob Rivers as one of the six distinct habitat categories in the Kalahari Gemsbok National Park. These river habitats or ecosystems have many features in common with the pan ecosystems but their differences are significant enough for them to be placed in separate habitat categories. The most important and fundamental difference between rivers and pans is that the rivers have open drainage as opposed to the endorheic drainage of the pans. The open drainage of the rivers results in an inflow of water and soil from outside the protected area into the protected area, the movement of water and soil downstream within the protected area, and the outflow of water and soil from the protected area.

Both the Auob and the Nossob cut through the overlying mantle of sand along their entire length in the protected area. These rivers are relics of a wetter epoch, although they still occasionally flow for a short period after very heavy rain in their catchments (Child, Parris & Le Riche 1971; Starfield, Shapiro, Furniss, Sears, Retief, Van der Walt & Mills 1982). Because they are dry for most of the time they are often referred to as "fossil" rivers or "dry" rivers.

The Nossob River varies considerably from north to south (Bothma & De Graaff 1973). It is a wide, shallow, sandy bed up to one kilometre and more wide, without calcrite outcrops, in the north and changes gradually to a narrow, fairly deep channel 100 – 500 m across, flanked with steep limestone banks in the south. It has a number of permanently dry tributaries (Fig. 1), cut off by transverse dunes, and the valley has a total area of approximately 72 km² (Bothma & Mills 1977). The course of the Auob cuts into limestone plains for much of its length. It is shallower in the north and cuts progressively deeper towards the south resulting in a channel some 40 m deep in the southern section.

The soils of the rivers are described by Werger (1978) as either silty, rocky or sandy. Silty or clayey soils everywhere cover the actual riverbeds. They are compact and poorly drained and are rich in nutrients, though there are considerable differences in the ionic concentrations in the soils in the two rivers which can probably be related to the different areas of origin of these rivers.

Local runoff water from the river banks after heavy rain or water flowing into the protected area from upstream results in temporary streams or pools in the river beds. The soils of the riverbeds are not as highly mineralized as the soils of pan
floors and salt-licks are not a conspicuous feature of riverbeds as they are on pan floors. There are, however, a few salt-licks in the calcrite cliffs of the Nossob River (Bothma pers. comm.).

Rocky soils occur commonly on the banks of the rivers where these are cut deep into thick, calcrite layers. The calcrite surface is usually weathered and there are frequent small pockets and fissures filled with gravelly white sand. The calcrite banks are usually rather steep, with slopes of 10 – 15°, and sometimes with vertical cliffs a few metres high in the upper parts. Rocky soils and cliffs are only found in rivers and on some pans in the Kalahari.

Belts of fairly shallow white sand typically occur on the slightly raised sides of the riverbeds between the calcrite banks and the silty central riverbed. These soils of washed sand possess a higher nutrient content than the red and pink sand and are underlain by compact substrates. Extensive pan-like areas occur in those slightly higher-lying portions of the riverbeds that are isolated from the river-course, and therefore, not influenced by the rare flood waters.

The vegetation in the rivers is similar to the vegetation found on pans and consists of dwarf-shrub communities or grassland communities (Werger 1978) with soil-type and rainfall determining the particular community. It is only on the floor of the riverbeds that a grassland community is found that is not found on the pans and vice versa. The vegetation in the rivers differs substantially from the savanna communities found in the sandveld and the plants growing in the river valleys are generally more nutritious than those growing in the sandveld (Kreulen 1980). The *Acacia erioloba* trees are also noticeably larger in the riverbeds than in the sandveld.

The rivers like the pans are characterized by a much higher faunal density than the surrounding sandveld. In Table 1 the mean year-round density of ungulates along a 40 km strip of the Nossob River and nearby dune or sandveld areas as determined by Mills (1982) illustrates the considerably higher overall density.

<table>
<thead>
<tr>
<th></th>
<th>Nossob River</th>
<th>Nearby Sandveld</th>
</tr>
</thead>
<tbody>
<tr>
<td>Springbok</td>
<td>1 655</td>
<td>2</td>
</tr>
<tr>
<td>Gemsbok</td>
<td>83</td>
<td>34</td>
</tr>
<tr>
<td>Hartebeest</td>
<td>152</td>
<td>10</td>
</tr>
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<td>9</td>
</tr>
<tr>
<td>Eland</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Steenbok</td>
<td>2</td>
<td>14</td>
</tr>
</tbody>
</table>

Table 1

*Mean year-round density of ungulates (animals counted per 100 km²) in a 40 km strip of the Nossob and nearby sandveld*
Starfield et al. (1982) also refer to the large herbivores' insatiable preference for the brackish areas in the rivers and pans of the Kalahari Gemsbok National Park and Bothma & Mills (1977) found the Nossob River to be an important wet season habitat for springbok, red hartebeest and gemsbok. They point out, however, that there is considerable movement between the river and the sandveld areas. As would be expected, the relatively high density of large herbivores in the rivers results in a correspondingly high density of large carnivores in the rivers and Mills, Wolff, Le Riche & Meyer (1978) observed 227 lions in the rivers compared with only 15 in the sandveld during regular counts between 1975 and 1976. Smithers (1971) showed that the majority of smaller mammals also favour the river habitats and the rivers have a higher overall density of smaller mammals than the sandveld, particularly on the river banks (Nel pers. comm.)

The rivers are shown to have a number of ecological features which make them important habitats or ecosystems within the overall Kalahari ecosystem. These include open water at certain times, compact and rocky soils supporting relatively nutritious vegetation and a relatively high faunal activity. Further research on the rôle of these rivers in the Kalahari ecosystem is, however, needed.

Although the rôle played by the biotic and abiotic components of the river ecosystem in the functioning of the system has not been specifically investigated, the similarities between pans and rivers are such that it can be postulated that similar self-maintaining and self-regulating mechanisms operate in the river ecosystems as in the pan ecosystems, with the difference in drainage being the major difference between the functioning of the two systems. This hypothesis needs investigating.

Artificial waterholes
There are two types of artificial waterholes in the protected areas, those fed from boreholes and earth dams or "gatdamme" that are excavated in clayey areas to hold local runoff water. Temporary pools after rain are a feature of riverbeds and pans and the earth dams in these areas serve to extend the period that this surface water is retained. Information about the distribution of these dams, and the water quality and period of availability, has not been published. The distribution of the permanent waterholes fed by boreholes is shown in Fig. 1. Pits or wells were also excavated in the rivers for watering stock and were used in the lower Nossob from 1908 until 1941, when the area was proclaimed as nature reserve (Child et al. 1971). The years in which some of the boreholes in the protected areas were equipped to provide water for wildlife are given by Child et al. (op. cit.) (Table 2).

The water in the boreholes is often highly mineralized and Child et al. (op. cit.) compared the concentrations of dissolved salts in borehole, trough and trough overflow water (Table 3). They found some variation in the concentrations of dissolved ions at some boreholes which they attributed to changes in wind velocity which govern the rate of pumping and so draw water originating from different geological formations. Martinelli & Hubert (1979) gave examples of this stratification and found that, near Nossob Camp, a generally saline water body with a salinity in excess of 5 000 ppm was found to saturate the sand below a depth of
approximately 75 m; and this saline water was overlain by lenses of marginally fresh water. These lenses were of varying thickness and possessed a salinity of approximately 1 500 ppm.

Table 2  
*The years in which some of the waterholes in the Kalahari Gemsbok National Park were equipped to provide water for wildlife*

<table>
<thead>
<tr>
<th>Waterhole</th>
<th>Year</th>
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<tbody>
<tr>
<td><strong>NOSSOB RIVER</strong></td>
<td></td>
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<tr>
<td>Unions End</td>
<td>1936</td>
</tr>
<tr>
<td>Grootkolk</td>
<td>1946</td>
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<tr>
<td>Lijersdraai</td>
<td>1958</td>
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<tr>
<td>Grootbrak</td>
<td>1958</td>
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<tr>
<td>Langklaas</td>
<td>1958</td>
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<tr>
<td>Kwang</td>
<td>1940</td>
</tr>
<tr>
<td>Diepboorgat</td>
<td>1966</td>
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<tr>
<td>Kaspersdraai</td>
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<tr>
<td>Dikbaardskolk</td>
<td>1940</td>
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<tr>
<td>Kameelsleep</td>
<td>1954</td>
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<tr>
<td>Jan se draai</td>
<td>1954</td>
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<td>Kransbrak</td>
<td>1954</td>
</tr>
<tr>
<td>Kijkij</td>
<td>1946</td>
</tr>
<tr>
<td>St. John’s Dam</td>
<td>1956</td>
</tr>
<tr>
<td>Rooiputs</td>
<td>1941</td>
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<tr>
<td><strong>AUOB RIVER</strong></td>
<td></td>
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<tr>
<td>Sitsas</td>
<td>1958</td>
</tr>
<tr>
<td>Craig Lockhart</td>
<td>1946</td>
</tr>
<tr>
<td>Dalkeith</td>
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<td>Groot Skrij Pan</td>
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<td><strong>DUNES</strong></td>
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<td>Gharagab</td>
<td>1963</td>
</tr>
<tr>
<td>Dankbaar</td>
<td>1963</td>
</tr>
<tr>
<td>Vaalpan</td>
<td>1965</td>
</tr>
</tbody>
</table>
### Table 3

Comparison of concentration of dissolved salts in borehole, trough and trough overflow water in the Kalahari Gemsbok National Park

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>SITE</th>
<th>DISSOLVED IONS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CO$_3^-$</td>
</tr>
<tr>
<td></td>
<td>Borehole</td>
<td>Trough</td>
</tr>
<tr>
<td>Kaspersdraai</td>
<td>x</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>139</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>596</td>
</tr>
<tr>
<td>Montrose</td>
<td>x</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>263</td>
</tr>
<tr>
<td>Kijkij</td>
<td>x</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>96</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>623</td>
</tr>
</tbody>
</table>
Child et al. (1971) confirmed the general observation that the wildlife makes considerable use of these waterholes, both in the rivers and in the sandveld, with the most marked influence on a particular species being the stabilization of a wildebeest population along the Auob River with its potable water. Bothma & Mills (1977) observed the establishment of a year-round population of wildebeest in the Nossob after new boreholes with more potable water were sunk in 1972 but suggest that a dry period is needed before any definite conclusions can be drawn about the permanency of this population.

Child et al. (1971) found that most species drank from waterholes along the Nossob and recorded the following maximum salinities accepted by the animals mentioned:

Jan se draai (42 579 ppm T.D.S.), springbok, gemsbok, and black-backed jackal (*Canis mesomelas*).

Kransbrak (38 942 ppm T.D.S.), wildebeest, steenbok (*Raphicerus campestris*) and secretary bird (*Sagittarius serpentarius*).

KijKij (26 637 ppm T.D.S.), ostrich (*Struthio camelus*).

Grootbrak (16 403 ppm T.D.S.), hartebeest.

Kaspersdrael (11 611 ppm T.D.S.), lion (*Panthera leo*), brown hyaena (*Hyaena brunnea*) and spotted hyaena (*Crocuta crocuta*).

Langklaas (9 175 ppm T.D.S.), Cape fox (*Vulpes chama*).

All species using the permanent artificial waterholes in the protected areas are found in the central Kalahari of Botswana where they are shown by Parris (1971) to survive without drinking water for long periods although wildebeest were only partially adapted to these conditions. The animals overcome the absence of open water in the Kalahari in one or more of the following ways (Parris op. cit.). They can be physiologically adapted to make efficient use of the moisture available to them. Although not much research has been done on Kalahari species, the principles underlying this type of adaptation have been illustrated in various desert animals, including large ungulates (Maloiy 1972). They can be behaviourally adapted by being able to recognize and dig up moisture-bearing bulbs and roots. There are numerous plant species in the Kalahari which have moisture-storing bulbs, roots or tubers and, because the sand is loose, animals are able to dig them up without much effort. A number of species, particularly the large herd species, can sense rain at great distances and move to where the rain has fallen and Parris (op. cit.) demonstrated how, in the Kalahari with its erratic rainfall, this facultative nomadic movement by animals achieves, in effect, both a higher and a more reliable rainfall for them.

The melon-like fruits of the gemsbok cucumber (*Acanthosicyos naudinianus*) the tsama melon (*Citrullus lanatus*) and other Cucurbitaceae are an important source of moisture to animals in the Kalahari. Because their production is governed by the particular rainfall pattern in the growing season, the distribution of available fruits varies considerably from year to year. Facultative nomadic movement by animals will, therefore, also increase effective availability of these fruits to them. Certain species, particularly birds, move right out of the area to avoid the driest periods (Maclean 1970).
Because the large ungulates are adapted to survive without drinking water for long periods, their use of the more highly mineralized artificial waterholes may be as much for the minerals as for the water itself and Bothma (pers. comm.) reports animals licking the salt-crystals at the overflow of highly mineralized waterholes. Over half the waterholes analyzed by Child et al. (1971) in the Nossob had salinity levels above the limits considered safe for beef cattle.

Child et al. (op. cit.) stated that, as veld deterioration due to wildlife or domestic animals often characterizes permanent artificial waterholes, the minimal disturbance of the vegetation in the northern and central regions of the Nossob measured in 1968 was remarkable. They found signs of prolonged high grazing pressure around some of the Auob and lower Nossob waterholes but, as these areas had a history of use by domestic stock, they suggested that wildlife may have been retarding the recovery of the vegetation after the stock had been removed, rather than being the primary cause of the reduction in vegetative cover. In the northern part of the Auob where resident wildebeest populations had become established around potable artificial waterholes, however, they found that the vegetation seemed to be suppressed.

Discussion and conclusions

Pans and rivers are natural features in the adjoining protected area of the southwestern Kalahari, whereas artificial waterholes are by definition unnatural. Pans are distinct ecosystems or sub-ecosystems in the larger Kalahari system and are characterized by compact and highly mineralized soils, endorheic drainage, relatively nutritious vegetation and a relatively high faunal activity. They make an important contribution to the system by considerably increasing spatial heterogeneity and by providing key habitats for many species. Because the pan ecosystem is actively maintained by the combined interaction of its biotic and abiotic components, its conservation requires the conservation of its components and the perpetuation of these interactions. One of the major interraactions essential for maintaining the system is the undisturbed use of the pans by herds of antelope and, since these herds are highly mobile, the protected area must remain large enough to enable this natural antelope-soil-plant interaction to continue.

The rivers are also distinct ecosystems or sub-ecosystems in the larger Kalahari system and have many features in common with pans. Like pans they also increase the spatial heterogeneity of the system considerably and provide key habitats for many species. Because they have an open drainage system, events in the catchments upstream of the protected areas which lead to changes in the natural stream flow or water quality, will influence the river systems in the protected areas. This makes their conservation in the protected areas potentially more difficult than the conservation of pans.

The ecological significance of artificial waterholes in the protected areas is poorly understood. Animals in the Kalahari are adapted to survive without drinking water for long periods and artificial waterholes are, therefore, not an essential source of moisture for them. In the case of highly mineralized waterholes, they are an additional source of minerals as well as water. Artificial waterholes may stabi-
lize populations of some species that are normally highly nomadic and may increase the faunal density in the vicinity of the waterholes. Artificial waterholes in the protected areas are a management tool and their use is governed by the management objectives for the areas.

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REFERENCES


