

# Palaeo and Present Ecological Value of the Etosha Pan, Namibia: An Integrative Review



by  
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**Titelphoto:** *Animals drinking at Gemsbokvlakte*

*Foto: Conny von Dewitz*

## Abstract

*This paper evaluates and synthesizes the past and present role of Etosha Pan and its significance to the surrounding ecosystem, much of it now zoned as a National Park for more than a century. The review incorporated here is drawn from cross-cutting results embracing and spanning the fields of geomorphology, hydrology, climate, soil and ecology. It emerged that the Etosha Pan provides direct and indirect (ecological) services and has an intrinsic ecological value to the park's ecosystem. Amongst other roles, the pan has a distinct influence on local climate, the distribution and abundance of wildlife and, in turn, on the tourism industry in the region. Huge flocks of flamingo, for instance, come to breed at Etosha Pan, and large herds of gemsbok, springbok, zebra, wildebeest, and giraffe are found in the terrain surrounding it. Although the Etosha Pan is an integral part of a large wildlife sanctuary and has been accorded a high conservation status due to its fragile ecology and importance to wildlife, nearly all of its significant catchment area falls beyond the protected zone. It is therefore imperative that as a necessary step in the conservation and functioning of its ecosystem, the catchment area of Etosha Pan be subjected to active ecological monitoring to help ensure its continued and beneficial existence.*

## Keywords

Etosha National Park, Semi-arid, Wildlife, Ecology, Savanna

## Introduction

Etosha Pan is a large (4760 km<sup>2</sup>, Lindeque & Archibald 1991) endorheic basin situated in north-central Namibia. It occupies approximately a fifth of Etosha National Park, which has a surface area of 22 700 km<sup>2</sup> (Mendelsohn *et al.* 2002). The Park is home to 114 mammals species, 340 birds species (<sup>1</sup>/<sub>3</sub> of which are migratory), and a variety of trees (Olivier & Olivier 1993). Much of the vibrant life that characterizes the park is concentrated within the fringes of Etosha Pan. It is on the plains adjacent to the pan that a large concentration of herbivores and their attendant predators eke out their existence. In turn, the booming tourism industry in the territory is in part reliant on this natural heritage. Thus, regular tourists to Etosha National Park are almost exclusively limited to the fringes of the Etosha Pan, where animal biomass reaches its maximum (Mendelsohn *et al.* 2002).

This paper is intended to review and place the ecological value of this depression into perspective. It commences with the geological and geomorphological setting of the area, followed by the palaeo-ecology of the region, which is deciphered from the available geological and geomorphological archives, albeit patchy. The present ecological value is then treated based on relevant research findings in the area.



The development of the modern-day Etosha Pan is attributed to the lost hydrological relationship with the Kunene River system. It is assumed that the endorheic upper Kunene River was diverted towards a pre-existing exoreic, lower Proto Kunene during the Mio-Plio- or Early Pleistocene active tectonic period (e.g. Jaeger 1926; Buch 1993; Kempf 2010). With the Cuvelai System being the only significant fluvial system remaining over the core of the Owambo Basin surface, the water body that was left behind underwent severe shortage of sediment and water input during the Pleistocene dry phases. Subsequently, the Cuvelai System concentrated its water budget and sediment load to a lobe of the former, larger lake, Lake Kunene. Following a period of calcrete formation, a much smaller Lake Etosha was gradually established. Since then, the lake underwent a history of fluctuating climatic conditions, with pluvial perennial phases during interglacials and dry episodes during glacials (Heine 1982; Buch, 1993; Kempf 2000; Hipondoka 2005). During the last 30 ka, for example, perennial lake conditions occurred several times as evidenced from fossils of semi-aquatic antelopes (Hipondoka *et al.* 2006) and stromatolites (Brook, Railsback & Marais 2011). Islands featuring today in the pan represents former shorelines deposits, as the pan, devoid of surface outlet, waxed and waned in response to varying climatic and hydrological conditions (Hipondoka *et al.* 2012).

Etosha Pan has a near-level horizontal surface morphology, subtly tilted to the east. Its major axis is oriented in the ENE – WSW direction (Jaeger 1926). The margins in the north and west of the pan are generally smooth with sandy beach ridges. The western margin in particular has a curved shoreline, punctuated in places by beach cusps. In contrast, the eastern edge is characterized by an irregular shoreline incorporating peninsulas with pronounced lacustrine cliffs, up to 20 m high in places. These edges are often capped with calcrete walls, with notable exception of the Mushara sand ridge at the north-eastern section of the pan. The southern edge is dotted with a number of springs and seepages, which are very popular to wildlife, particularly during the dry season (e.g. Bigalke 1961). Sediments of the pan are almost exclusively made up of silt and clay, which accounts for over 90% (Hipondoka 2005).

## **Present Climate and Hydrology**

Based on the average annual figures of precipitation and temperature, Berry (1980) distinguished three climatic periods at Etosha. In his classification, January to April is a wet and hot season, followed by a dry and cold season starting from May and lasting until August. The remainder of the year is considered as dry and hot. This makes Etosha region, like most of the country, a summer rainfall area with almost completely dry winters. Evaporation is estimated to exceed rainfall by a factor of 8.4 at Okaukuejo (Engert 1997).

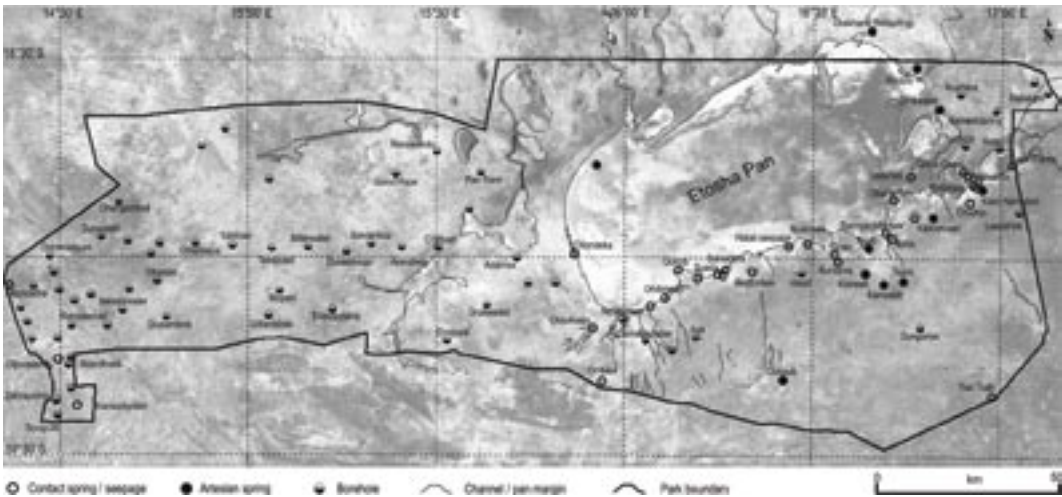


Figure 2: Types (contact spring, seepage, artesian spring, and borehole) and distribution of waterholes in the Etosha National Park. (Data source courtesy of Etosha Ecological Institute, supplemented from Auer (1997).

Background image: Landsat mosaic, courtesy University of Maryland.

Rainfall is highly variable in terms of quantity, timing and coverage. The eastern part of the park receives an annual average rainfall varying between 550 and 600 mm. An average amount of 300 mm is received in the western section (Mendelsohn, el Obeid & Roberts 2000). These rainfall averages reflect the precipitation gradient of the region, which increases from west to east. However, Etosha Pan has been considered to have an effect on this rainfall gradient, where an abnormally high rainfall occurs some 30 km west of the Etosha Pan, before it decreases again after a ground distance of 50 km (Hipondoka, Versfeld & Kapner 2004).

The elevated rainfall in that region, devoid of any environmental factors such as topographically high ground that could induce orographic rainfall, is attributed to the Etosha Pan, which is situated upwind of that area. Along with tentative evidence of a possible positive feedback mechanism involving rainfall and dust variability (Brooks & Legrand 2000) it is hypothesized that speedy winds encouraged by uninhibited ground friction of the barren Etosha Pan warms up the incoming moist-bearing air and drives it further west. The vegetation in the west would then help decelerate the wind speed, which in turn cools down the air. This would help in allowing condensation to take place. Additionally, possible dust particles in suspension, derived from the surface of the Etosha Pan (Bryant 2003; Washington *et al.* 2003) may act as nuclei for condensing the water vapour. Ultimately, the combined effect of these processes appears to be a localized higher rainfall at some distance in the leeward of the Etosha Pan. Coupled with the general rainfall gradient, the consequence of enhanced rainfall in that area is that the driest plains in the park are situated immediately west of Etosha

Pan. As discussed below, the dry season range of migratory herds of ungulates that dominate the animal biomass in the park is centered on these driest plains, west of the Pan.

Surface inflow into the Etosha Pan comes mainly from the Cuvelai System in the north, with some of its headwaters in the region of Serra Encoco, a southern spur of the central Angolan Highlands located east of Cassinga (Stengel 1963). Perennial tributaries only occur in Angola (Stengel 1964) and inflow into the Etosha Pan only takes place in exceptional flood years (Lindeque & Archibald 1991) as recently occurred between 2008 and 2011. Approximately 75% of Etosha's water comes from the Cuvelai System, while the rest of the inflow mainly comes from the *omiramba* (*sing. omuramba*) Owambo and Omuthiya to the east (Lindeque & Archibald 1991). Because of the Otavi Limestone with its shallow rendzic and lithic soils found south and southwest of the Etosha Pan, most of the rainwater received in that area infiltrates into the karst system and there is little surface drainage from that direction (Bigalke 1961). For that reason, groundwater flows towards the Etosha Pan from the south, feeding a significant number of springs (contact and artesian) and seepages along or near the southern edge of the pan (Figure 2). Surface drainage from the west is no longer connected to the pan and now terminates into Adamax Pan, located some 10 km to the west of Etosha Pan. However, the existence of a popular Okondeka fountain located at the margins of and flows for hundreds of meters into the pan (Berry *et al.* 1998) is attributed to groundwater inflow from Adamax Pan.

## Soils and plant communities bordering the Etosha Pan

Reconnaissance soil and vegetation of the Etosha National Park was done by Le Roux *et al.* (1988). Soils around the Etosha Pan were grouped into two main classes. The area situated on the south and south-west of the pan is covered with calcrete rubble on the surface. Calcareous loamy soils are found in the west of the pan, whereas carbonate-free Arenosols derived from Kalahari sands blanket the area north and east of the pan. More recently, Beugler-Bell & Buch (1997) mapped soils of the park using a locally adapted Food and Agriculture Organization (FAO) system. Soils of the Etosha Pan itself are mapped as *calci sodic Solonchaks* to *sali calci Solonetz*s. The Andonivlakte, a floodplain situated in the northeast lobe of the pan, has soils of *stagnic Solonetz*, with a structural B-horizon. *Cambic* and *ferralic Arenosols* developed in deep sandy substrata are found in areas north, northeast, and northwest of the pan. Along the western and north-western edges of the pan, (hyper) *calcaric Regosols* to (hyper) *calcaric Arenosols* and *aplic Calcisols* are the soils dominating those areas. Extremely shallow to shallow clayey-loamy soils, which developed from limestone, characterize the area south and southwest of the Etosha Pan (Beugler-Bell & Buch, 1997).

Le Roux *et al.* (1988) recognized the positive spatial correlation of the vegetation distribution and soils in the park. Significant parts of the Etosha Pan itself are largely devoid of

vegetation, due to its high sodium content. Communities of tall grasslands are found along the western margin of the Etosha Pan, the Ekuma River, Poacher's Point Peninsula, and marginally at the Andonivlakte. The extensive grassland bordering the southern edge of the pan was classified as 'sweet grassveld on lime'. This unit is locally interspersed with stands of woody plant communities, such as *Acacia nebrownii* (Le Roux *et al.* 1988), which, in Bigalke's (1961) view, implies a sparse pioneer community. It is the most utilized vegetation unit in the park, comprising less than 10% of the conservation area (Le Roux *et al.* 1988). The large and abundant population of herbivores that it supports, particularly when good rains falls, is said to be attracted by its sweet, short grassveld (Berry & Louw 1982; Le Roux *et al.* 1988).

## Palaeo-ecological value of the Etosha Pan

The ecological significance of the past environment in and around the Etosha Pan is vouchsafed from the paleontological record of the area. Much of this archive was discovered through studies aimed at understanding the fluvial and climatic environment of the region (e.g. Martin & Wilczewski, 1972; Heine 1982; Smith & Mason 1991). Specifically, a very high turnover of various fossil fragments and artifacts found in the area and highlighted below suggest that the environment of Etosha Pan was characterized by a richer diversity of landscape patches and higher productivity associated with abundant and perennial surface water.

The first reports of fossils from the immediate environment of Etosha Pan were on stromatolites found at Poacher's Point Peninsula, Pelican Island, and some other localities in the eastern part of the pan (Martin & Wilczewski 1972; Rust 1984; Smith & Mason 1991; Buch 1993). These stromatolites, consisting of at least six growth shells, are believed to have been constructed by cyanobacteria in very low-energy lacustrine conditions (Smith & Mason 1991). At that time, their age was not firmly established, due in part to challenges associated with dating carbonate residue. They were recently resolved by Brook *et al.* (2011) through double dating of carbonate and organic residue trapped in the same stromatolite, and established that carbonate ages were 15 - 21 ka older. Calibrated ages for organic material range from 3 - 19 ka. This signifies the existence of perennial lake conditions in the recent past.

More recently, three assemblages of fossils belonging to a variety of large mammals and fish have been discovered at Etosha Pan (Hipondoka 2005; Pickford *et al.* 2009). These fossils include animals that still exist at Etosha National Park, while the distribution of others is now restricted to areas with permanent water in the sub-continent, such as the Okavango Swamps. Fossils found around the Oshigambo Peninsula which represent animals that still exist in the Etosha region includes *Struthio camelus* (ostrich) egg fragments, bones belonging to *Antidorcas marsupialis* (springbok), *Aepyceros melampus* (impala), and *Taurotragus oryx* (eland). Added to this list are fossils of the now extinct equid, *Equus quagga* (quagga),

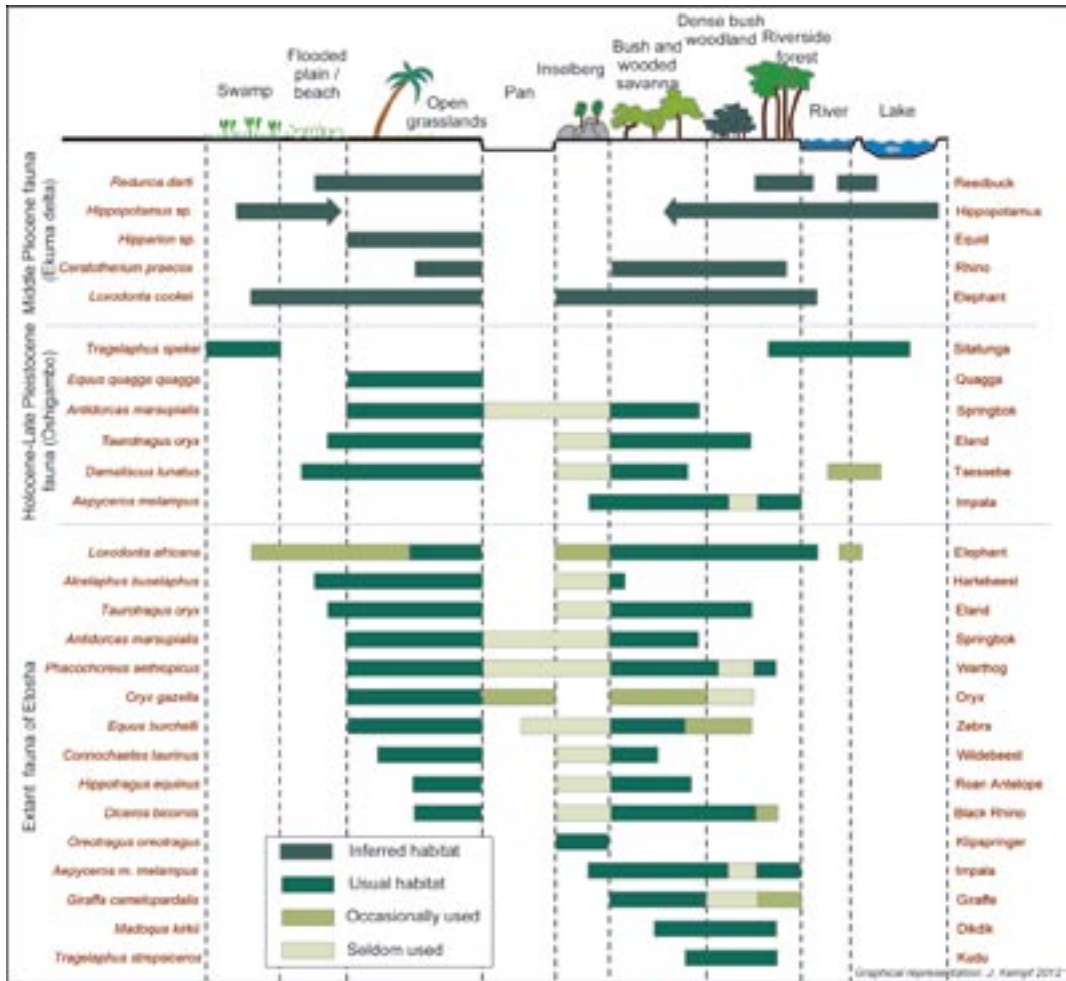


Figure 3: Schematic habitat preferences of selected mammals (past and present) based on Skinner & Smithers (1990) at Etosha National Park. Most species listed above the dotted line are only known to exist at Etosha from fossil records; thus they represent an environment that differs remarkably from present day habitats. The sitatunga and the reedbeek riverine antelopes as well as hippopotamus are especially ecological indicators for persistent lake conditions and higher local rainfall. Most species listed below the dotted line exist today in the park. The shift to the wetter side in the fossil collection is apparent.

of *Damaliscus lunatus* (tsessebe), and *Tragelaphus spekei* (sitatunga) (Hipondoka 2005; Hipondoka *et al.* 2006). These fossils were dated to the Late Pleistocene (Pickford *et al.* 2009) and mid-Holocene (Hipondoka, 2005).



Other fossils dating back to the Middle Pliocene were discovered in the Ekuma River system and the northern edge of the pan. Pickford *et al.* (2009) documented fossils of *Bellamya unicolor* and *Mutela* (freshwater clam), *Crocodylus* sp. (crocodile), *Phoenicopterus ruber* (greater flamingo), as well as extinct taxa including *Struthio daberasensis* (ostrich), *Loxodonta cookei* (elephant), *Ceratotherium praecox* (rhinoceros), *Hipparion* sp. (proto-horse), *Hippopotamus* sp. (hippopotamus) and *Redunca darti* (reedbuck). A third sample collected from the Etosha Pan member of Andoni Formation date from the Late Miocene, ca. 6 Ma, and also include *Mutela*, *Clarias* sp., *Pelusios* sp. *Cyclanorbidae*, *Crocodylia*, *Phoenicopterus ruber*, *Loxodonta cookei*, and additionnal *Panthera cf. leo* (lion), a suid and an antelope *Damalacra acalla* (Pickford *et al.* 2009; Miller *et al.* 2010).

Effectively, these assemblages of fossils mentioned above reflect a rich mixture of browsers and grazers. This in turn suggest that the area surrounding Etosha Pan enclosed well-developed woodlands and floodplains bordering with a lake spanning millions of years as summarized in Figure 3 in accordance to habitat preference of noted species. The existence of permanent water is evidenced from the presence of sitatunga already referred to above, known as the most aquatic of antelopes, but also from crocodile, hippopotamus, tsessebe, and the *Redunca* species (Skinner & Smithers 1990), as well as by fish, aquatic mussels, snails and turtles. *Reduncini* are generally poor dispersers and encompass a high fidelity for this very special habitat, due to their unique adaptation to exploiting highly productive floodplain and wetland habitats. Similarly, sitatunga exhibit most extreme adaptations of the *Reduncini* to a semi-aquatic life style (Cotterill 2000). These persistent floodplain grazers are fully depended on perennial wetlands with bog and floating bog grasslands. Essentially, the dynamics of the area appear to have been rooted in the presence of Lake Etosha, which, as evidenced from the fossil records, played a vital role in supporting and maintaining a rich and diverse wildlife population in the region.

Hitherto, no Early Stone Age implements were found in the area mainly because of severe lack of typical raw materials such as silcrete or silicified country rock. Unpublished data of the authors shows some later Middle Stone Age tools from Etosha sites, particularly at Pelican Island and Poacher's Point. These artefacts were made from white greasy quartz and quartzite forming relatively dense pavements on well-developed reddish palaeo-soils. Materials were most likely transported from Damara outcrops of the Kaoko Belt by the early occupants. Implements from chalcedony and ostrich eggshell beads, representing the wide-spread Namibian Later Stone Age, were also found on surface sites surrounding the pan. Earliest known inhabitants of the area are hunter-gatherers, the Khoisan speaking Hei//om. Collectively, it is therefore apparent that Etosha Pan was a center of diversity during the late Cenozoic with a core of shrinking and expanding habitats as also modeled by Kempf (2000).

## Present Ecological Value of the Etosha Pan

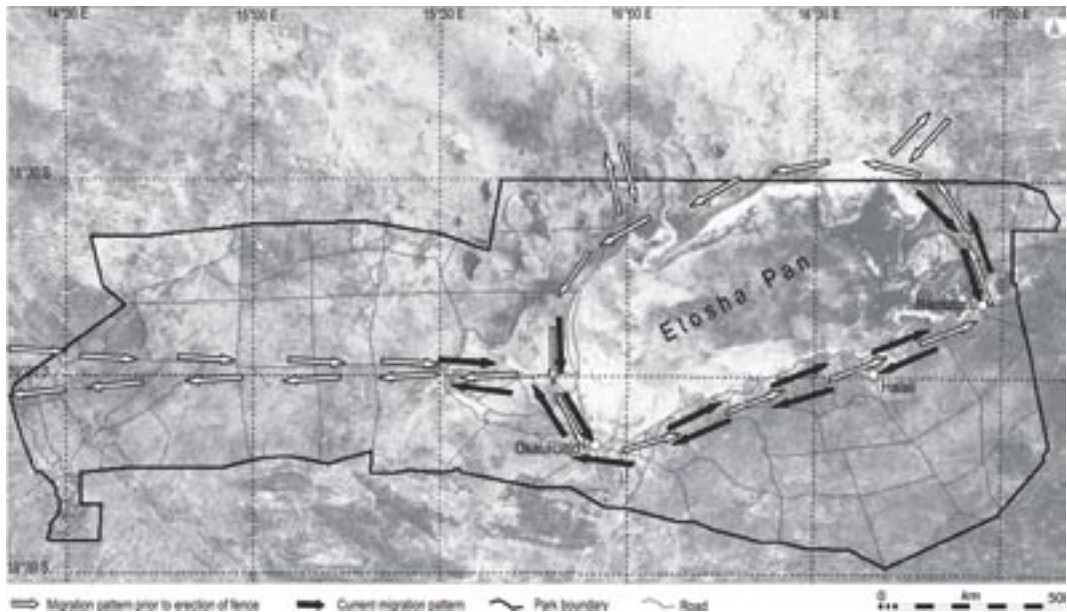


Figure 4: Migration patterns of plain ungulates around the Etosha Pan, mainly from east to west after the first major rainfall in the area, before and after the erection of the fence along the park perimeter (Migration pattern prior to the erection of fence redrawn after Tinley 1971).

Background image: mosaic of Landsat TM, courtesy University of Maryland

Although the geologically recent phase of drying up of Lake Etosha, which resulted in the current play, has adversely affected the diversity of wildlife in the area as presented above, anecdotal historical evidence recognizes its immediate surroundings to have the highest density of mammalian herbivore biomass amongst the semi-arid regions of the world today. In the terrain surrounding the pan, animal density is in excess of 70 large animals per square kilometer (Mendelsohn *et al.* 2002). In the recent past, however, the animal density was much higher. The number of wildebeest and plain zebra, for example, was estimated to 25 000 in 1954 and 22 000 in 1969, respectively (Berry & Siegfried 1991). The numbers have since dwindled, currently totalling only about 2500 wildebeests and 5000 zebras (Mendelsohn *et al.* 2000).

Several studies have attempted to address the causes of such major reduction in the number of plain ungulates. Although there are disagreements in details, these studies generally attributed that reduction to disease (i.e. anthrax), declines in rainfall and increases in anthropogenic influence (e.g. fencing) (e.g. Tinley 1971; Berry 1980; Ebedes 1981; Turnbull *et*

*al.* 1989; Berry & Siegfried 1991; Lindeque 1991). Nevertheless, with 114 mammal species and 340 bird species (Olivier & Olivier 1993), the faunal diversity in Etosha National Park is extraordinarily high for a semi-arid to sub-arid savanna. In essence, this suggests that the current wildlife population at Etosha is essentially a remnant of a much larger and even more diverse fauna. Interestingly, most of the ungulates and their attendant predators are found along the fringes of the Etosha Pan, whereas the migratory birds come to take advantage of the seasonal inundation of the pan under current climatic conditions.

Before the park was gradually fenced off and finally completed in 1973 (Berry 1997), the most profound feature around the Etosha Pan was the anti-clockwise annual migration of the great herds along the northern perimeter of the Etosha Pan (Figure 4; Tinley 1971). Prior to the erection of this fence, animals migrated from east to west with the start of the first rains and moved back to the east towards the end of the rainy season (Tinley 1971). Animals from the north also joined the rest of the herds on the plains west of the Etosha Pan during the rainy season (Bigalke 1961). In adjusting to the new measures introduced by the fence, which effectively curbed and restricted movements of most large animals to the park, animal migration at present follow a clockwise migration route along the southern edge of the pan, with some remaining in the east. Their wet season concentration in the west is generally centered on the plains of Okaukuejo-Okondeka-Adamax triangle, with a spillover to the O'Mbari plains (Figure 2).

The annual migration of springbok, zebra and wildebeest from the eastern to the western part of the Etosha Pan and surrounding plains has been ascribed to the availability of rainwater and grazing (Bigalke 1961; Tinley 1971; Le Roux *et al.* 1988). Unlike perennials during the growing period, annual species found predominantly in the western side of the Etosha Pan are considered to have a high feeding value, a situation that gets reversed during the dry season. The palatability of annuals during the wet season is also enhanced due to a lack of durable remains of the plants of the previous year from which perennial species start their new growth (Le Roux *et al.* 1988).

The implication of rainwater in such a seasonal movement sounds like a paradox, because rainfall decreases from east to west in the park, as described above (Engert 1997). Moreover, the plains on the north and west of Okaukuejo where animals migrate with the onset of the first rains are known to be the driest in the park (Hipondoka *et al.* 2004). This migration of large herds after the first rains is remarkably quick and may take place almost overnight or within days (Bigalke 1961). The herds then remain concentrated in these plains for the duration of the moist and hot season (Ebedes 1981). As the grass dries and becomes dormant, and the rainwater desiccates, animals spread and return gradually to the perennial water sources, particularly along the southern and eastern edge of the pan, near perennial springs and seepages (Bigalke 1961; Le Roux *et al.* 1988; Auer 1997). No migration takes place in dry years as recently observed during the 2012/2013 rainy season.

The mechanisms that trigger wildlife migration have long been debated in the past, particularly at the Serengeti where the largest annual migration of large herds of ungulates in the world takes place. Like at Etosha, animals migrate from the wetter (exceeding 1100 mm p.a.), northern part of the Serengeti to the driest (at about 500 mm p.a.), southern section situated in the rain shadow of the Ngorongoro Highlands (Wolanski *et al.* 1999). The proposed environmental factors governing this migration in the Serengeti are reviewed by, amongst others, Maddock (1979), Belsky (1995), and Sinclair (1995), and include higher nutrients and safe refuge from predators offered by the short-grass communities of the drier part. Grasses in the southern (drier part) plains are also said to have more nitrogen and calcium for lactating females (McNaughton 1990). Adding to that list is the animals' dislike of wet and muddy soil in the northern savannas during the rainy season or simply the natural animal instinct in fully utilizing total plant productivity in the park (Jarman & Sinclair 1979). Wolanski *et al.* (1999) pointed out that none of the above models has explicitly included rainfall, and that they also failed to consider unused forage and to accurately predict the timing of the migration, which may vary by as much as three months. Thus, in their contribution to the environmental mechanisms that govern such annual migrations, Wolanski *et al.* (1999) have instead concluded that water quantity and quality is the most influential factor in the Serengeti. Specifically, they have linked the migration to the wetter part of the park to high salinity level, which in turn is a function of dilution by rainfall.

When comparing the above-mentioned findings from the Serengeti with the environmental factors that have been explicitly invoked at Etosha, the only resonance between the two ecosystems is the nutrient content. No seasonal difference has been identified in the water quality at Etosha, for example, between waterholes located in the plains north and west of Okaukuejo, where animals concentrate during the wet season, and those in the rest of the plains where they spend the dry season (Winter 1985; Auer 1997). Rainfall could be regarded as the other consistent parameter; but it is treated in all the studies, both at Etosha and at the Serengeti, as a background role player, triggering key variables such as primary production, and not as a driving force in its own right.

In both ecosystems, plain ungulates migrate to the driest area with suitable habitat. The plains to the north and west of Okaukuejo are situated in the leeward (with respect to prevailing north-easterly wind) of Etosha Pan, which, as described above, has been hypothesized to influence the local climate of that area (Engert 1997; Hipondoka *et al.* 2004). Similarly, the wet season range in the Serengeti is located in the rain shadow of the Ngorongoro Mountains. It is therefore probable that migrant animals simply move to the driest parts with a suitable habitat within their range as a way of seeking shelter from excessive rains. This assumption is particularly strengthened by the fact that migration to their respective wet season range usually takes place within days following the onset of the first good rains, and that in the event that the rain starts earlier or is delayed, the animals respond accordingly by moving later or not at all (e.g. Sinclair 1995). Assuming that this hypothesis holds true, the annual

migration of ungulates at Etosha should be closely linked to the influence of the Etosha Pan on the local climate, in close association to the rainfall gradient.

As stated earlier, approximately a third of the 340 bird species that found at Etosha is migratory. Lesser and greater flamingos are amongst the migratory birds that flock to the pan each year specifically for breeding (e.g. Archibald & Nott 1987; Berry 2000). This makes Etosha Pan one of the only two inland sites in southern Africa (the other is the Makgadikgadi Pans in Botswana) where flamingos breed in large numbers. For that reason, the pan has recently been declared a Ramsar site (Kolberg, Griffin & Simmons 1997).

Flamingos are the only species of a family, embraced in the Order *Phoenicopteriformes*, which is one of the evolutionary oldest and persistent bird groups still existing today. Fossils of flamingos have been found in sediments from as far back as the Early Tertiary (Scott 1975); they also feature in the fossil record of Etosha (Pickford *et al.* 2009). What attracts flamingos to Etosha Pan for breeding is its leveled topography, clay sediments of high salinity/alkalinity and the availability of seasonal water (Berry 2000). Such climatic and environmental conditions allow, among others, the flourishing of blue-green algae and microscopic invertebrate, which form the main diet of these water birds (Berry 2000). There are six species of flamingos, but the lesser and greater flamingos are the only African types (Scott 1975; Berry 2000). The continual conservation of their habitat at Etosha therefore is significant for preserving the regional population of flamingos.

The presence of a large aggregation of wildlife on the fringes of Etosha Pan is also of economic value by means of the tourism industry. Four out of five tourist camps in the Etosha National Park are situated within a 10 km radius from the Etosha Pan. The closest camps to the pan are Onkoshi, Namutoni and Okaukuejo, sited near natural springs, where animals come in large number for watering, or the pan's margin. The number of tourists in the park has been steadily on the increase, averaging 10% annually since 1990. In 1998, for example, the combined total of overnight visitors to the park was just under 200 000, up from about 85 000 visitors in 1991 (Mendelsohn *et al.* 2000). Undoubtedly, the concentration of wildlife within the fringes of Etosha Pan is what drives the tourism industry in the region.

The importance of the Etosha Pan to the tourism industry is also evidenced by the location and distribution of roads traveled by tourists in the Etosha National Park. Approximately 75% of all tourist road segments lie within the 10 km radius from the Etosha Pan. Thus, the underlying factor sustaining this tourism sector is essentially the habitat, which in turn is inherited and rooted in the presence of Etosha Pan and its previous status as a lake.

## Conclusions

The fossil record suggests that Etosha Pan and environs is a natural ecosystem with a long history of a rich and diverse wildlife. Although its past glory of perennial lake conditions has given way to a dry, barren landscape, the pan regulates indirectly the distribution of wildlife in the park through the presence of permanent springs and seepages, as well as grass plains around its fringes. It further influences annual animal migration in the park due to its impact on the local climate. Scientific understanding of abiotic environment, such as the seemingly barren Etosha Pan, is therefore of primary importance to the conservation of biodiversity.

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