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The Return of the Giants: Ecological Effects of an Increasing Elephant Population

Northern Botswana and adjacent areas, have the world's largest population of African elephant (*Loxodonta africana*). However, a 100 years ago elephants were rare following excessive hunting. Simultaneously, ungulate populations were severely reduced by decrease. The ecological effects of the reduction in large herbivores must have been substantial, but are little known. Today, however, ecosystem changes following the increase in elephant numbers cause considerable concern in Botswana. This was the background for the "BONIC" project, investigating the interactions between the increasing elephant population and other ecosystem components and processes. Results confirm that the ecosystem is changing following the increase in elephant and ungulate populations, and, presumably, developing towards a situation resembling that before the reduction of large herbivores. We see no ecological reasons to artificially change elephant numbers. There are, however, economic and social reasons to control elephants, and their range in northern Botswana may have to be artificially restricted.

INTRODUCTION

Many of the large African rivers flow through areas, that, for at least part of the year, are devoid of other surface water. In such areas, animals that are water dependent may aggregate at the permanent water in the dry season and disperse in the wet season to areas with temporary water supplies and higher quality and/or quantity of forage. Almost certainly, this is how the ecosystem around the Chobe River functioned for millennia. About 150 years ago, however, the Chobe system changed. Hunting of elephants for ivory had been practiced for at least 1000 years (1), but on a small scale and, presumably, within a sustainable level. With increasing markets in the 19th century the hunting of elephants increased (1, 2), and towards the end of the century elephants were rare in Botswana. The Chiefs and the Protectorate Authorities reacted by imposing regulations on hunting of elephants, and in the 1930s elephant numbers began to increase (2, 3). Today, the elephant population in northern Botswana and adjacent parts of Zimbabwe and Namibia is estimated to more than 100 000 animals (4), constituting the largest population on the continent (5). Mean density of elephants along the Chobe riverfront in the dry season is about 4 animals per km², dropping to ca. 0.5 per km² during the wet season, when elephants disperse southwards drinking from temporary pans (6).

About the same time as the elephant population reached its nadir, other changes took place. Rinderpest, a disease spread by cattle, came to Africa in 1887 and reached Botswana in 1896–1897, causing heavy mortality in wild and domestic ungulates (1). In addition, both species of rhinoceros (*Ceratotherium simum* and *Diceros bicornis*) were wiped out, or virtually so, by hunters. During the 1930s and again in the early 1950s, timber was extracted from the woodlands along the Chobe River, and a sawmill and a village were built on the riverfront (7).

There is almost no documented evidence of vegetation com-

position and structure along the Chobe River before the elephants and the rhinos disappeared and rinderpest caused major decline in ungulate populations. However, the changes caused by the decline of megaherbivores and other large herbivores must have cascaded through the ecosystem, affecting soils, vegetation, herbivores, and predators. Changes in fuel load, caused both by alterations in herbivory regime and as a result of timber extraction, probably increased fire frequency (3).

We know slightly more about the ecological processes associated with the recovery of elephant and ungulate populations. The resulting habitat modifications have caused concern in Botswana about potential adverse effects on the area's biodiversity and for the loss of scenic woodlands along the river (8, 9). Both factors have implications for the region's lucrative tourist industry. In particular, the loss of the *Acacia* woodlands along the riverfront (10) and the decline since the 1960s of the Chobe bushbuck (*Tragelaphus scriptus ornatus*) (8) are sources of concern for conservationists and park managers. The increasing elephant population obviously plays a role in these changes, and the "Chobe elephant problem" has been given highest priority in nature conservation and management by Botswana authorities; the ultimate question being: to cull or not to cull (11, 12). However, there is some uncertainty about the ecosystem processes associated with the increasing elephant population.

BOTSWANA NORWAY INSTITUTIONAL COOPERATION AND CAPACITY BUILDING PROJECT (BONIC)

In an effort by Botswana Department of Wildlife and National Parks (DWNP) to improve the preconditions for management of wildlife resources, the Botswana Norway Institutional Cooperation and Capacity Building Project (BONIC) was established in 1998 and ran for 5 years. The project was based on cooperation between DWNP, the Norwegian Institute for Nature Research (NINA) and the Centre for International Environment and Development Studies (Noragric) at the Agricultural University of Norway. The project had a threefold aim: *i*) to provide formal and informal research training to DWNP staff (7 MSc and 4 PhD students have been or are being trained within the project); *ii*) to carry out research that improves the understanding of the ecosystems in northern Botswana and the systematic changes that are taking place, and *iii*) to encourage and facilitate the use of the improved knowledge and staff capacity by DWNP in the management of wild natural resources.

There have been many studies on the Chobe elephants (6, 13–17) and their impact on trees (3, 18–20). However, less is known about the wider ecological implications of the elephant activities, including the interactions with nutrient availability and distribution, vegetation dynamics, distribution and behavior of other mammals and biological diversity and species richness (9, 21, 22). Therefore, BONIC was not specifically studying elephants, but rather elephant – ecosystem interactions (23).

BONIC consisted of seven interrelated studies or subprojects (Fig. 1), most of them run by one Norwegian researcher and one DWNP counterpart and/or a PhD or MSc student. The topics of

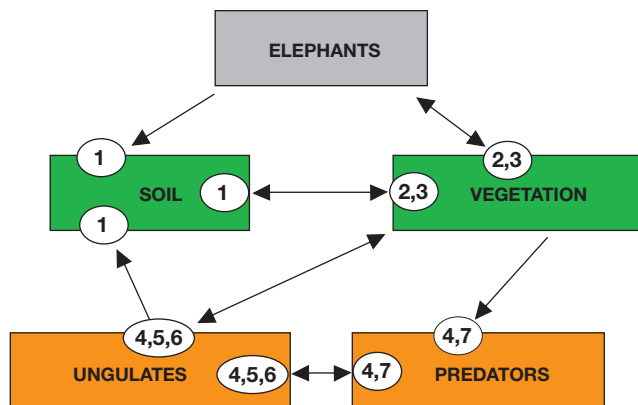


Figure 1. A schematic picture of the Chobe ecosystem and the research areas for the BONIC subprojects, referred to by the numbers from the list in the text.

the subprojects were:

- To quantify the relationships between elephants: and
1. soil properties and nutrient cycling;
2. herbaceous vegetation composition and grazing;
3. woody vegetation structure, composition, regeneration and browsing;
4. distribution and community composition of mammals and gallinaceous birds;
5. population ecology and behavior of impala (*Aepyceros melampus*);
6. behavioral ecology of buffalo (*Syncerus caffer*);
7. population ecology of lions (*Panthera leo*).

During the first three years the project also included a socio-economic component (24, 25).

The project had a common core study area, which was photographed from the air in 1998. Based on the photographs a map of the six main habitat types was constructed, including floodplain, riparian forest, *Capparis* shrubland, *Combretum* shrubland, mixed woodland and *Baikiaea* woodland (Fig. 2). Five transects (old fire breaks) run south from and perpendicular to the river through the core area. Along each of the 5 transects permanent sampling sites were established, in total 13 sites in the *Capparis* shrubland and 15 in each of the other habitat types except the riparian forest fringe that was too fragmented to sample in this way. The following is an outline of the project, showing some of its results and conclusions.

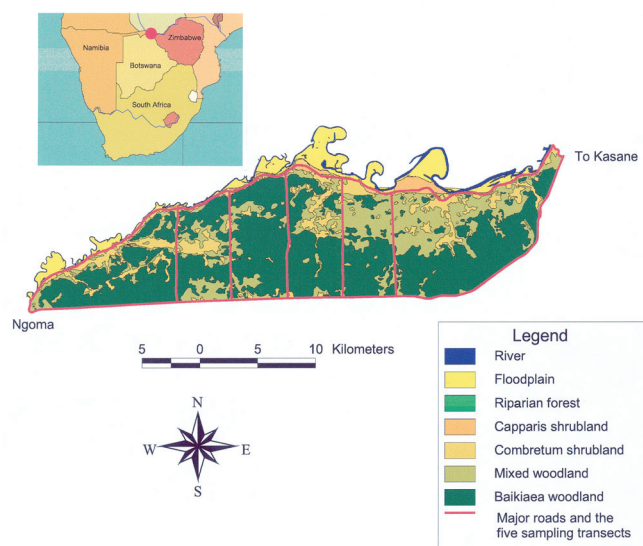


Figure 2. Habitat map over the core study area at the Chobe river front showing the 6 recognized habitat types, major roads and the 5 common sampling transects. The narrow fringe of riparian forest is barely visible on the map.

PAST AND PRESENT VEGETATION

To quantify the relationship between vegetation and large herbivores, we described the woody and herbaceous vegetation and its current use by elephants and other large herbivores. Present vegetation was also compared with historical records, in order to describe the changes taking place primarily since the 1960s, when elephants were again becoming common in the area. Vegetation was analyzed in the 73 permanent sample sites along the five transects. For herbaceous plants and woody plants < 0.5 m tall, canopy cover per species was recorded in five plots of 1 m² at each site. For the tree layer, including woody plants > 0.5 m tall, density of trees by species and height and canopy cover for each tree were recorded in one 400 m² plot at each site. In addition, in 2003, we re-analyzed the vegetation transects analyzed by Simpson in 1969/1970 (10) and Addy in 1992 (8).

The seasonally inundated floodplains are today dominated by the grazing-tolerant, strongly rhizomatous perennial grass *Cynodon dactylon* and the grazing-resistant, sharp and stiff *Vetiveria nigritana*. These obviously grazing-adapted grasses were not listed by Simpson (10) as dominant floodplain species in the area in 1969/1970, when grazing pressure was lower than today. The narrow strip of riparian forest (hardly visible in Fig. 2) along the river was already reduced by the time of Simpson's study (10), and only fragments remain today (26). The elevated alluvial plains between the floodplains and the Kalahari sand ridge were described by Selous (27) in 1874 as an open flat with widely scattered clumps of bush and with large *Acacia* trees at the edge of the river (the riparian forest fringe). This description is from the time when elephant numbers were declining and before the rinderpest outbreak. A hundred years later, when elephants had increased again, Simpson (10) described the elevated alluvial plains as a degrading riverine tree savanna with large *Acacia*- and *Combretum* trees and a well-developed shrub layer. Today, most of the large trees are dead and the area is covered by *Capparis* shrubland, dominated by *Capparis tomentosa* and *Combretum mossambicense* (Fig. 2).

Very limited information is available from old written sources about the woodland vegetation on Kalahari sand dominating further away from the river. However, there is evidence (Skarpe et al. unpubl. data) that some shrub species and the large tree species, including *Baikiaea plurijuga*, have decreased within some kilometers from the river since Simpson's study (7) in 1969/1970. Instead there has been an increase in some smaller tree species. A comparative study of aerial photographs from 1962, 1985, and 1998, covering the period of major increase in elephant numbers, showed a general decline in woodlands and a corresponding increase in shrub vegetation (26, 28). Today, *Combretum* shrublands dominate in the transition zone between sand and alluvial soils, followed by mixed woodlands with scattered large *Baikiaea plurijuga* and many smaller tree species, and *Baikiaea* woodland furthest away from the river. Recent data from the sampling sites along the transects and from the aerial photography (Fig. 2) indicate that distribution of habitats may be governed by interactions between soil resources (Table 1) and herbivore impact.

Table 1. Levels of selected nutrients in four habitat types in Chobe National Park*. Shrubland includes *Capparis* and *Combretum* shrublands.

Habitat	Calcium (cmol kg ⁻¹)	Phosphorus (ppm)	Organic Matter (%)	pH
Floodplain	14,2	9,1	2,4	4,7
Shrubland	3,8	13,1	0,7	6
Mixed woodland	1,1	4,4	0,4	5,1
<i>Baikiaea</i> woodland	1,06	2,2	0,4	5

*Masunga and Dhillon unpubl. data.

The herbaceous vegetation in the woodlands is dominated by grasses of the genera *Aristida* and *Digitaria*, as also recorded by Simpson (10), but in addition we found *Panicum maximum*, an excellent fodder grass, among the dominants. Most grass species in the woodlands are perennial, and species composition varied little with interannual variation in rainfall. Ordination of the data on herbaceous vegetation using Detrended Correspondence Analysis (29) shows the gradient in community composition along one of the transects (Fig. 3).

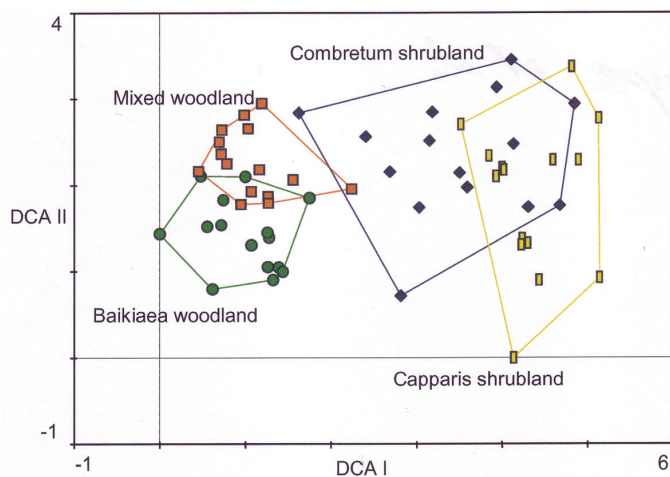


Figure 3. Ordination (Canonical Correspondence Analysis) of the herbaceous vegetation in one of the transects showing the gradient in species composition from the *Baikiaea* woodland (green) to the mixed woodland (red), *Combretum* shrubland (blue) and *Capparis* shrubland (yellow). Symbols indicate sampling plots, 5 at each site.

WOODLAND REGENERATION

The concern about the reduction in woodlands cover has focused on the visible impact by elephants and fire on mature trees (3, 18, 19). However, to maintain a healthy tree population, a reduction of life span of mature trees is less important than the lack of regeneration and of recruitment of new individuals into the reproductive population (30). We found seedlings and saplings of woody plants to be rare and the soil seed bank small (< 100 viable seeds per m²) in all habitat types (31). In the riparian forest fringe the soil seed bank had about five times more viable seeds in areas with relatively low elephant impact than in heavily impacted areas, and the species composition was different (31). The similarity between the aboveground flora and the seed bank flora was low, as is often the case. Potential reasons for the low rate of sexual reproduction could be predation on seeds and/or seedlings by insects, rodents or larger mammals (31) or depletion of symbionts, e. g. mycorrhizal fungi, in the soil following the death of the mature trees.

There has been special interest in the lack of regeneration of the riverine *Acacia* woodlands on the elevated alluvial flats. Studies at Lake Manyara in Tanzania have shown that *Acacia* tree populations are unable to regenerate during periods of high impala density due to intense seedling predation (32). We found local impala densities higher than 150 animals per km² in some areas along the Chobe riverfront. To test the idea that seedling predation by impala is an important reason for the lack of regeneration of trees on the elevated alluvial plains along the Chobe riverfront (33), an enclosure experiment was performed. Seedlings were planted in areas with different impala densities in *i*) complete enclosures, ca. 6 m²; *ii*) semipermeable enclosures, ca. 6 m², open below 0.5 m above the ground allowing access by small animals like birds, rodents and baboons (*Papio ursinus*); or *iii*) in unfenced control areas. Seedlings were of four tree species, two species that have increased in density in the area since the studies of Simpson (10) and Addy (8), (*Croton megalobotrys* and *Combretum mossambicense*) and two species that have de-

creased in density during the same period (*Faidherba* (formerly *Acacia*) *albida* and *Garcinia livingstonei*). Growth rate, tissue loss and mortality of the seedlings were recorded and related to treatment and density of impala in the area. Preliminary results show that browsing by large herbivores, e. g., impala, plays an important role in predation on tree seedlings close to the river (34).

Thus, written evidence shows that the huge *Acacia* trees, for which the Chobe riverine woodlands were famous in the 1960s (10), established after Selous' visit to the area in 1874 (27), and were already old and dying without regeneration in 1969 (7). Both the written evidence and our experiment suggest that these *Acacia* trees were derived from a cohort of seedlings established some 100 years ago, when populations of elephants, impalas and other browsers were low. The experiment further predicts that with high ungulate densities some tree species may not be able to regenerate in most of the riverine habitat. Such species may depend on local refugia like steep riverbanks, and on natural dynamics of herbivore densities, caused, e. g., by drought or disease, for persistence in the area.

GRAZERS AND BROWSERS

Herbivore-induced changes in vegetation composition may take either of two fundamentally different directions (30), leading to an increase in fast-growing palatable species or in slow-growing, often chemically defended, unpalatable species (Fig. 4).

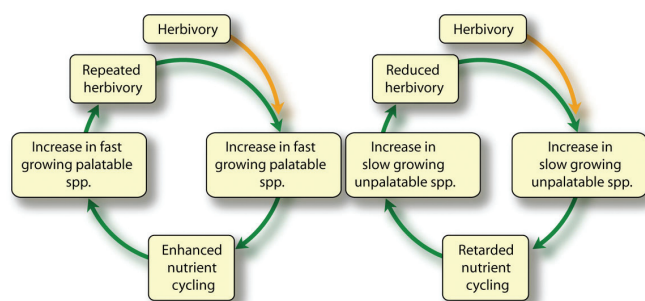


Figure 4. Browsing by ungulates may lead to the dominance either of fast growing, palatable species (a) or of slow growing, often defended, unpalatable species (b), with different implications for nutrient cycling, heterogeneity of resource availability and further browsing.

We used both observational studies and controlled experiments with simulated and real browsing to study the interactions between large herbivores, plant traits and changes in plant species composition in the relatively nutrient-rich alluvial soil and on the relatively nutrient-poor Kalahari sand. In the sampling sites along the transects signs of grazing and browsing were recorded. For the tree layer the number of twigs of 8 mm diameter (= average elephant bite diameter (16)), current season's shoots, bites by ungulates on current season's shoots and bites/breaks by elephants were counted on each tree. Results show a strong gradient with generally increasing herbivore impact from the *Baikiaea* woodland to the shrublands. The data also reveal considerable differences between elephants and ungulates in foraging pattern and in response to the herbivory-induced vegetation changes. Whereas elephant browsing pressure (% of trees utilized) was highest in the mixed woodlands and *Combretum* shrublands, ungulate browsing pressure (% of shoots utilized) peaked in the *Capparis* shrublands. This pattern may be caused partly by the low availability of browse for elephants in the shrublands compared to the woodlands, but also reflects a difference between elephants and ungulates in browse-species preference. Some of the tree species that have increased in density in the *Capparis* shrublands since the studies by Simpson (10) and Addy (8), e.g., *Capparis tomentosa* and *Combretum mossambicense*, are intensely browsed by ungulates like impala and kudu, but are

avoided by elephants. Elephants, on the other hand, selectively browse some of the *Combretum* species increasing on the Kalahari sand (Skarpe et al. unpubl.). Elephant impact was also found to be higher in areas of more undulating terrain compared to relatively flat areas (35).

ELEPHANTS AND MICROBES

One of the most important ways by which large herbivores interact with their environment is by affecting nutrient distribution and availability (30). In most terrestrial ecosystems, the majority of the net primary production enters the decomposition subsystem as plant litter. However, in savanna ecosystems fires, insects or large herbivores may consume considerable amounts of aboveground biomass.

Selective herbivory may influence species composition of the vegetation and hence quantity and quality of plant litter. Generally, litter from fast-growing plants or plant parts decompose rapidly, whereas litter from slow-growing plants decomposes slowly and may cause immobilization of nutrients in the soil (36). Thus, the herbivory-induced increase either in fast-growing or in slow-growing species may lead to positive feedback loops *via* changes in the nutrient cycling rate (30; Fig. 4).

A pilot study on decomposition of litter from three different tree species was undertaken in the different habitat types. Results so far indicate that weight loss in litter assumed an exponential trend with a steep rise when monthly average temperature and humidity are high. Differences in decomposition rates between tree species have been recorded (Fig. 5). Rates of losses based on total dry matter will be correlated with loss rates of different nutrients in the litter and soil. Knowledge of the different rates of decomposition of plant species can indicate the spatial pattern of nutrient distribution. The results so far suggest that the different habitats may represent different nutrient cycling states within the landscape (Masunga and Dhillion, unpubl. data).

ELEPHANTS AND OTHER HERBIVORES

By influencing vegetation structure and composition as well as the fire regime, elephants may change the availability and distribution of food and shelter for other herbivores (37). We followed community composition and habitat utilization of mammals and gallinaceous birds in order to trace effects of the changing habitats. A trapping survey of small mammals (less than 2 kg) in the mixed woodland (38) showed that the species composition of the small mammal community varied greatly over short distances. Apparently, this is in response to small-scale variation in vegetation composition and structure, often created or enhanced by large herbivore activities like trampling, digging, defecation and urination.

Density and distribution of mammals larger than 2 kg and of gallinaceous birds (e. g., guinea fowl) were studied using the methodology described by Buckland et al. (39) and Motsumi (40). Ten transects, run-

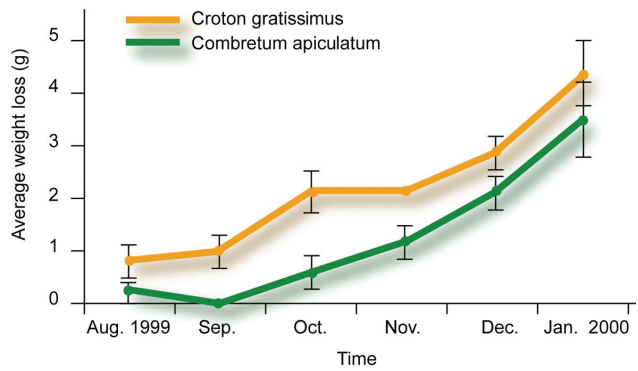


Figure 5. Decomposition rate of leaves of two different tree species in *Baikiaea* woodland. Figures are weight loss in g (mean \pm S.E.) per month.

ning parallel and perpendicular to the river, were driven during the wet and the dry season in the morning, evening and night, using spotlights. More ungulate species were present in the dry season than during the wet season (Fig. 6). Ordination with Canonical Correspondence Analysis and Redundancy Analysis (28) showed significant positive correlation between elephant

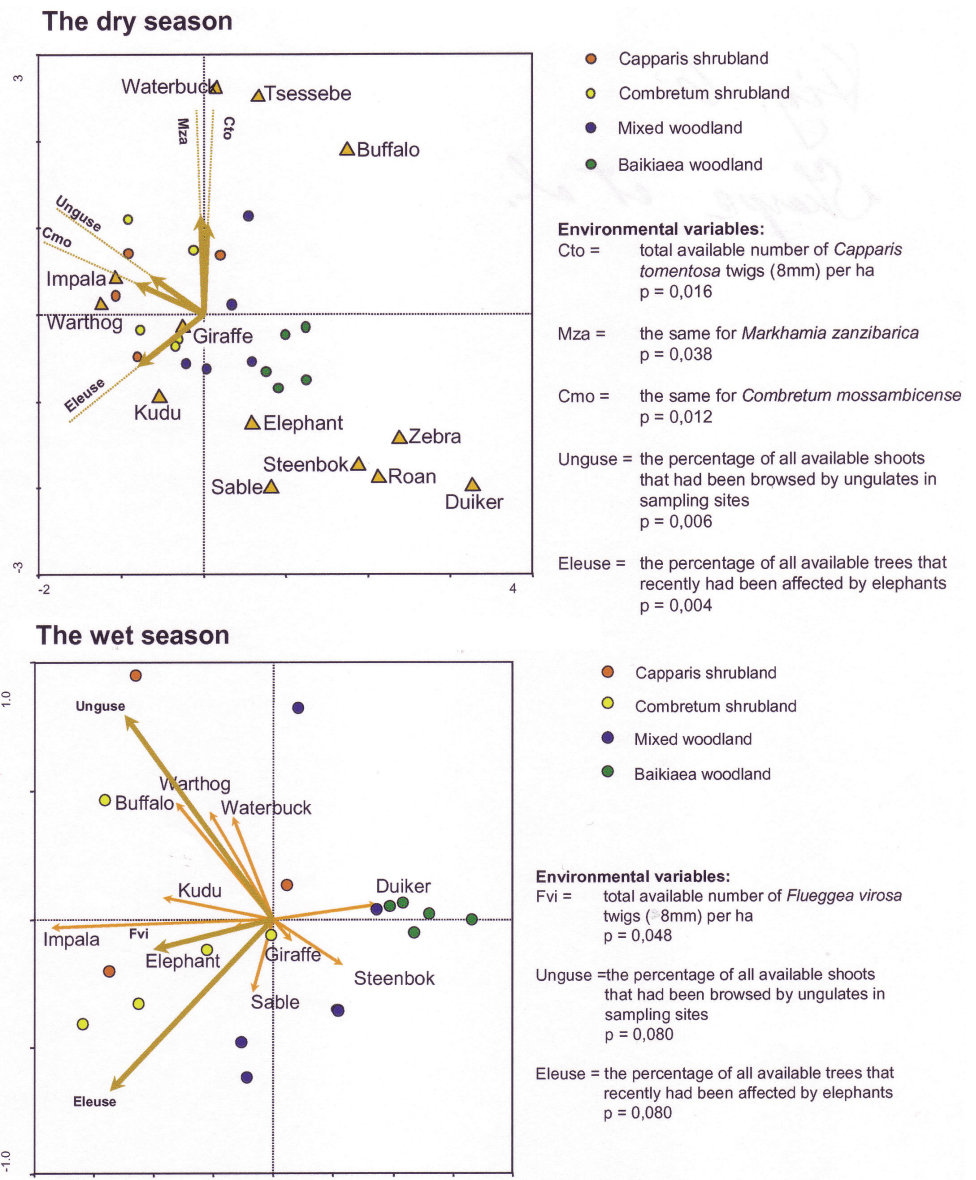


Figure 6. Canonical Correspondence Analysis (CCA) – triplot diagram of species, sampling sites and significant environmental variables during the dry season (upper) and a corresponding Redundancy Analysis (RDA) – triplot for the wet season (lower). Habitat types, sample transects and environmental variables are explained in the Figure.

impact, availability of certain tree species much browsed by ungulates, ungulate browsing pressure and the distribution of ungulate species (Fig. 6). Both in the wet and the dry season about half the ungulate species exhibited a positive correlation with elephant impact, measured as % of woody plants recently browsed or broken by elephants (Stokke et al. unpubl.; Fig. 6).

Impalas remained primarily in the heavily elephant-impacted *Capparis*-, and *Combretum* shrublands the whole year. As an indicator of impala population performance and to study juvenile mortality, 80 newborn lambs have been radio collared, 20 per year from 1998 to 2001. Births were highly synchronized in mid-November. The influence of rainfall (amount and distribution in space and time) on the annual production of impala lambs is being investigated. Results indicate that juvenile mortality is low, and that the numbers of impala are increasing along the riverfront (33). One plausible explanation for the increase in impala densities is the increase in palatable shrubs like *Combretum mossambicense* and *Capparis tomentosa*.

Impala population data were also used in a bio-economic model (24) indicating a high potential value of the animals for local communities both for nonconsumptive and, outside the Chobe National Park, consumptive use. Such utilization

within ca. 60 km of the dry season ranges (Fig. 7).

While it has long been known that male buffalo move in and out of herds, cows have been considered to remain within their natal herd all their lives (43, 44). Our study has showed that a large proportion of the Chobe females switched herds, and some emigrated long distances (up to 133 km (45)).

During the time of the study, buffalo maintained good body condition throughout the year, and the population structure suggested a slow increase in numbers instead of the previously assumed decline (46). This suggests that buffalo were not limited by competition with elephants or smaller ungulates for food. In our study, both dung analyses (46) and isotope analysis (unpubl. data) indicate that buffalo at Chobe browse very little, limiting potential dietary competition to grazing. A study in the dry season found elephants avoided areas of floodplain recently grazed by buffalo, while buffalo preferred areas of floodplain recently grazed by elephants (46). Thus, there is no evidence that elephant grazing at Chobe reduces food resources for buffalo, but some indication that grazing by buffalo may adversely affect grazing resources for elephants, a conclusion supported by Prins (44) and Van de Koppel and Prins (37).

A FLUCTUATING LION POPULATION ON THE CHOBE RIVERFRONT

Lion populations are assumed to be regulated by food and social factors. The impact by elephants on vegetation may influence lion populations directly by changing visibility and accessibility during hunts, and indirectly by changing density, population structure and/or the behavior of prey animals.

In the project we were able to follow the whole resident riverfront lion population by radio tracking eight collared females in five different groups and the three pride males present in the area. We monitored data on space and habitat use, food intake, social interactions, cub production and loss of individuals by regularly tracking and observing the lion groups over four years.

The results show that the riverfront lion population was divided in semi-independent groups of females and young, arranged linearly along the heavily elephant-impacted riverfront. Data on prey selection suggest that buffalo and elephant calves constituted a significant proportion of the diet both during the wet and dry season. The lion population size varied considerably through our four years of study (> 60%). Even though birth rate and cub survival appeared to be high, and may have created short-term increase in population size, it was not large enough to avoid occasional decreases in population size. In some periods the lion population was so small that it was highly vulnerable to stochastic demographic events. The main reasons for the observed decreases in population size may be summarized as: *i*) The litter sex ratio has been significantly male biased resulting in a high proportion of dispersing sub-adults; *ii*) high human-induced mortality among pre-dispersing sub-adults, e.g. poaching and traffic accidents; *iii*) emigration of female groups; *iv*) lack of immigration; and *v*) infanticide. Only one immigrant lion has been observed during our four years of study. This was an adult male that took over as a pride male for some of the female groups and killed their cubs. A female biased sex ratio in the adult segment of the population and low immigration rate have posed a question regarding the extent of isolation and inbreeding of the Chobe riverfront population (47). This question is being addressed by genetic analyses of tissue samples.

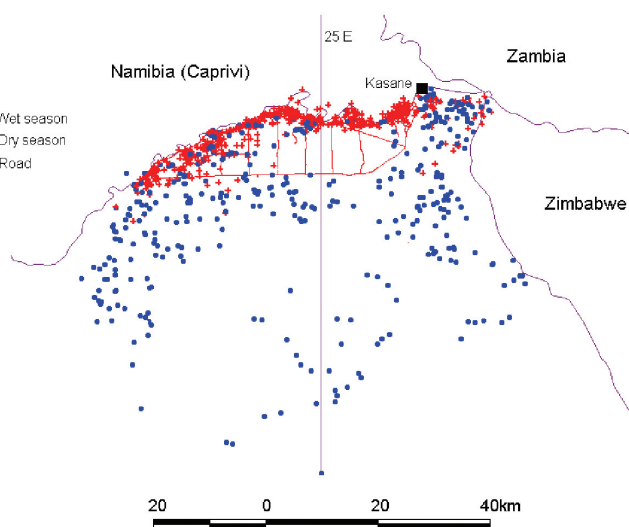


Figure 7. Distribution of buffalo in the dry (red crosses) and wet (blue dots) seasons. Each point represents one location of a herd (which may contain more than one collared animal).

would, however, in most cases require improved organizations for Community Based Natural Resources Management (25).

At the start of the project the Chobe buffalo population was believed to be in decline (41), and the possibility that competition with elephants was the underlying cause was discussed by conservationists and management authorities. Buffalo are the second most important large herbivore in the ecosystem in terms of biomass, after the elephant, and, like the elephants, most of the population leaves the river front in the wet season. To gain a better understanding of the movement pattern of buffalo, 20 females and 20 males were radio collared during the first two years of the project. Figure 7 shows a summary of movement data over 19 months. During the dry season the buffalo were concentrated along the riverfront in large herds numbering up to 1300 individuals. In the wet season buffalo dispersed into the woodlands south of the core area, drinking at temporary pans. At this time the large herds broke up into smaller groups of ca. 50 – 200 animals (42). Although this population has been reputed to move as far as Nxai Pan, ca 200 km south, we found no evidence of seasonal long distance movements. Wet season ranges of the population were confined to

DYNAMICS OF THE CHOBE ECOSYSTEM

The changes in vegetation structure and composition recorded during the last ca. 50 years along the Chobe riverfront are assumed by local people, conservationists and scientists to be caused mainly by the increasing elephant population (7, 8, 10–12, 19). Such changes have been reported from many areas with increasing elephant activity (21, 48–50), and may involve alterations in tree size structure (49) and/or tree species composition (50). However, while elephants selectively destroy mature trees, the density and species composition of tree regeneration may be determined by fire and/or predation on seeds or seedlings (31, 32, 34, 48, 51). While fires were important in the Chobe riverfront ecosystem following the logging operations and when herbivore densities were low (3), they are now uncommon within our core study area (26, Skarpe unpubl. data), although they have significant impact on woodland structure and composition further away from the river (19, 46).

Other factors that could have contributed to the observed ecosystem changes include alterations in water availability. There are indications that the availability of surface water has decreased in southern Africa during the last ca. 100 years (refs in 1 and 52). Still, Tyson (52) did not find any regional trend in rainfall during the period for which records are available (since ca. 1910; 52). Reduced water availability would, of course, negatively affect woody vegetation. However, it can not explain both the establishment of the riverine *Acacia* woodlands after the 1870s and their subsequent decline and replacement with shrubs from the 1960s. Further, the strip of riparian forest, of which only fragments are left in most places, is still comparatively intact close to settlements, where animal impact is reduced. We, therefore, conclude that the declines and later increases in the elephant and antelope populations are the main cause for the vegetation changes described.

While changes in structure and composition of vegetation following herbivory are readily described, we are only beginning to understand the impact of large herbivores on ecosystem processes. Herbivory-induced changes in vegetation composition may lead to dominance of species with different growth rates and leaf chemistry, compared to the former dominants. This influences litter quality and quantity and, therefore, nutrient cycling and resource distribution (30). Eventually, this is expected to have feedback effects on the herbivores themselves. How such feedbacks may operate depends on which direction the vegetation changes take: towards species that are slow-growing and unpalatable or towards species that are fast-growing and palatable (Fig. 4). Our data on woody vegetation and browsing give no evidence of a decrease in palatability of woody vegetation in the heavily elephant-impacted areas. The distribution patterns of mammals (> ca 2 kg) and gallinaceous birds exhibit concentrations in the most impacted areas close to the river, which for highly mobile species like birds and larger mammals can not be explained by the vicinity to water only. Further, we recorded an increase in populations of buffalo (46) as well as in impala (34), and older records (3, 7) suggest a long-term increase in populations of buffalo, impala and greater kudu. This is contrary to the findings of Fritz et al. (53), who analyzed wildlife censuses from 31 conserved African ecosystems and concluded that elephants negatively affected populations of browsers and mixed feeders, but had no influence on grazers. One reason for this Chobe paradox may be the intermittent pattern of herbivory. Intensity of browsing and grazing is highest during the dry season, when plants largely are dormant, and lowest in the wet growing period, when many animals disperse away from the riverfront. Another contributing factor may be a net import of nutrients from the wood-

lands to the shrublands and floodplains close to the river, as elephants forage mostly in the woodlands but spend considerable time each day drinking and socializing close to the river, and, thus, deposit large amounts of faeces and urine there.

ARE THERE TOO MANY ELEPHANTS?

The density of elephants in the Chobe area before the large-scale ivory hunt in the mid- and late-19th century is not known. Campbell (2) used Parker and Graham's (54) equation for calculating elephant densities from rainfall, soil types and human population. He estimated the number of elephants in the whole of Botswana in the beginning of the 19th century to be between 200 000 and 400 000 animals, with the highest densities in the mesic north. Perhaps, there never was an equilibrium between woodland vegetation and elephants, but instead multiple stable states, with transitions triggered, e. g., by periodic droughts, or a stable limit cycle, in which elephant densities increased while eating down the vegetation, then declined because of a shortage of food until low elephant density allowed the vegetation to recover, and elephants again increased (51, 55, cf. 56). Such dynamics probably cascade through the whole ecosystem, and may in the long term facilitate the coexistence of species with different environmental requirements. If this hypothesis is valid, man can create an artificial equilibrium by locking the system in a state of low elephant density (55), but this may in the long term lead to loss of biological diversity.

Much of the Chobe elephant problem has concerned the role of elephants in the disappearance of the riverine *Acacia* woodlands on the elevated alluvial plains along the Chobe River. As we have shown, these woodlands were probably a transient artefact, caused by artificially low densities of large herbivores following rinderpest and excessive hunting of elephants about 100 years ago, creating a window of opportunity for seedling establishment. Now that these woodlands have all but disappeared, their re-establishment would require drastic reductions in herbivore populations, including not only elephants, but also smaller browsers like impala (32–34, 37, 57).

Our studies have confirmed that the ecosystem along the Chobe riverfront has changed profoundly since the 1960s, probably reverting towards a situation somewhat similar to the one before the excessive hunting of elephants and the rinderpest panzootic. There is, however, little evidence of a reduction in the carrying capacity for other large herbivores, in fact the dominating species of browsers, grazers and mixed feeders have increased in numbers concurrently with the elephants. This does not, of course, mean that habitat conditions have not declined for some species, such as bushbuck. We do not, however, see any ecological reason to artificially change the number of elephants in Chobe National Park, either through culling or opening new dry season ranges by providing extra water from boreholes (58). Nevertheless, there are social and economic reasons to limit the distribution of elephants in Botswana, and it may be necessary to draw limits to the permissible elephant range, destroying groups that emigrate beyond those boundaries. This would relieve human-elephant conflict while providing the opportunity for a sustainable harvest of such "surplus" animals and the marketing of various commodities, as far as international rules will allow.

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