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The Zambezi Society and The Biodiversity Foundation for Africa are working as partners within the African Wildlife Foundation's Four Corners TBNRM project. The Biodiversity Foundation for Africa is responsible for acquiring technical information on the biodiversity of the project area. The Zambezi Society will be interpreting this information into user-friendly formats for stakeholders in the Four Corners area, and then disseminating it to these stakeholders.

THE BIODIVERSITY FOUNDATION FOR AFRICA (BFA is a non-profit making Trust, formed in Bulawayo in 1992 by a group of concerned scientists and environmentalists. Individual BFA members have expertise in biological groups including plants, vegetation, mammals, birds, reptiles, fish, insects, aquatic invertebrates and ecosystems. The major objective of the BFA is to undertake biological research into the biodiversity of sub-Saharan Africa, and to make the resulting information more accessible. Towards this end it provides technical, ecological and biosystematic expertise.

THE ZAMBEZI SOCIETY was established in 1982. Its goals include the conservation of biological diversity and wilderness in the Zambezi Basin through the application of sustainable, scientifically sound natural resource management strategies. Through its skills and experience in advocacy and information dissemination, it interprets biodiversity information collected by specialists like the Biodiversity Foundation for Africa and uses it to provide a technically sound basis for the implementation of conservation projects within the Zambezi Basin.

THE PARTNERSHIP between these two agencies was formed in 1996 as a result of mutual recognition of their complementarity. They have previously worked together on several major projects, including the biodiversity component of IUCN's Zambezi Basin Wetland project and the evaluation of biodiversity in Tete province described in detail in the first Four Corners TBNRM Biodiversity Information Package.

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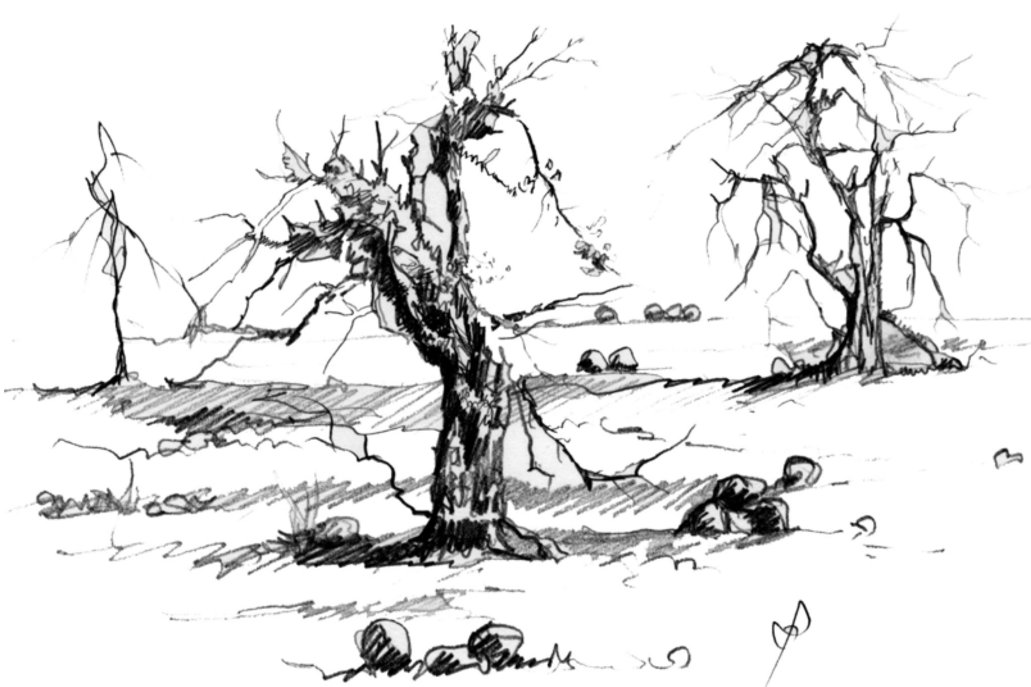

CHAPTER 15. ELEPHANT IMPACTS ON VEGETATION AND OTHER BIODIVERSITY IN THE BROADLEAVED WOODLANDS OF S-CENTRAL AFRICA

A.M. Conybeare

15.1 INTRODUCTION

The Four Corners Transfrontier Conservation Area covers about 290,000 km^2 centred on Victoria Falls, and includes parts of northern Botswana, eastern Caprivi, south-east Angola, south-west Zambia and north-west Zimbabwe. This area contains the largest single savanna elephant (*Loxodonta africana africana)* population in Africa in the largest area of contiguous elephant habitat, making it a very important element in conservation planning. The elephant population is thought to be about 175,000 animals (Hoare, Chapter 14) and there is no absolute barrier to elephant movement.

As a step towards understanding the conservation implications of this population, which will probably increase in size, a review is given of the impacts of elephants on their environment. To take into account as much of the existing relevant information as possible, the review extends outside the Four Corners area to cover most of south-central Africa. In the consideration of impacts on biodiversity other than vegetation, it has been necessary to draw on sources outside even this larger area.

15.1.1 Study Area

This review focuses on the broad-leaved woodlands, shrublands and wooded grasslands of south-central Africa from southern Tanzania to South Africa and Angola to Mozambique, roughly corresponding to White's "broad-leaved woodland and wooded grassland" and also Ansell's "southern savanna zoogeographical zone" (both in Cumming 1982). The *Acacia*- dominated areas of East Africa, the arid zone of the Namib, Kalahari and northern Cape, and the sclerophyllous shrubland of the southern Cape province of South Africa are excluded from detailed consideration. Mean annual rainfall ranges from 500 mm to more than 1400 mm in a few isolated localities, with most of the area receiving between 600 and 1000 mm. In parts of southern Africa, particularly areas bordering the Kalahari, frost can be a factor affecting vegetation.

The elephant population of the entire south-central Africa area is estimated to number about 200,000 animals (Barnes *et al.* 1999). Within this area, elephants have a discontinuous distribution in many protected areas, communal areas and on private land.

15.2 ELEPHANT IMPACTS ON THE ENVIRONMENT

The major impact of elephants is on the vegetation, primarily through their feeding habits, but they also make paths, dig to open up water sources, consume large volumes of water and affect nutrient cycling by depositing large quantities of urine and dung. Elephants eat both grass and woody plants but tend to obtain the bulk of their food in the dry season from woody plants. As most grazing is done in the wet or growing season, and grasses can quickly replace foliage removed, the impact of elephants on grasses is generally assumed to be low (Barnes 1983a, Owen-Smith 1988).

With increasing human populations the area available to elephants has been reduced and they have become more confined to protected areas. The combination of range compression and reproductive increase in protected areas in the absence of hunting pressure, has led to increasing numbers of elephants in these areas and their impact on the vegetation became a cause for concern. However, although this concern appears to be a relatively recent development, the impacts of elephants were noted long before this century. In 1681, Ludolphus wrote in *A New Historie of Ethiopia* of elephants "laying waste to a forest" (in Spinage 1994). In South Africa, Pringle noted in 1819 that elephants uprooted large numbers of *Acacia* trees, and Gordon Cumming, hunting in what is now eastern Botswana in 1848, noted many trees being uprooted (in Spinage 1994).

The general effect of increasing density of elephants has been a reduction in the amount of woody vegetation and an alteration of the structure of forest and woodland towards shrubland and wooded grassland. Such gross changes to vegetation also have implications for other species, and for ecosystem processes such as nutrient cycling and soil-water relations. Biodiversity is thought to be promoted by heterogeneous environments. If elephant utilisation of vegetation increases habitat heterogeneity, then the impact of elephant at low densities may serve to increase diversity, while at higher densities the reverse probably holds (Owen-Smith 1989, Western 1989). Seed dispersal is a positive result of elephant feeding and in Hwange National Park (NP) in Zimbabwe, seeds of 27 woody species and one palm were found in elephant dung (Dudley 2000). Germination of seeds of some species may also be facilitated by passage through the elephant's gut and subsequent deposition in dung (Hanks 1979).

15.2.1 Impacts on Woody Vegetation

When feeding on woody plants, elephants are capable of feeding very delicately or causing gross destruction. The effects of elephant utilisation are often referred to as "damage"; in this review the term is used to refer to any removal of woody biomass, and not only to suggest excessive destruction.

When feeding on shrubs, where the foliage is within easy reach, elephants generally pull off leaves and twigs, sometimes tearing off branches. With smaller plants, the stems may be broken off just above the ground or, with seedlings, the entire plant with the roots may be pulled out. Subterranean plant parts are also not safe from elephants as they will excavate to expose roots and other parts, for example tubers of favoured plants in sandy soils (Williamson 1975). With larger trees, where the foliage is beyond reach, trees may be uprooted or pushed over or the trunk or large branches may be broken off. Shallow-rooted trees are likely to be pushed over without breaking and frequently continue to grow in a horizontal position. With deeper rooted trees the stem is likely to be snapped and coppice growth may be produced from the stump. Both results may even be seen in the same tree species, perhaps depending partly on soil type. Elephants eat the bark of many trees, which they tear off in long strips or break off in pieces depending on the tree species. If bark is removed around the complete circumference of the trunk, the tree will die above the ringbarked point. Even if not completely ringbarked the exposed wood will die and be attacked by insect borers, which often leads to the premature death of the tree. Baobabs are an exception to this as a different vascular structure enables them to survive ringbarking.

Since elephants feed in a selective manner, the first species to show the impact of elephant utilisation are those species that they favour. The impact on large trees usually causes concern first as it is conspicuous and large trees are aesthetically appealing.

The effects of elephants will now be looked at in the various areas in which impacts have been investigated in south-central Africa, starting with the Four Corners area. The results are summarised in Table 15.1, but it is not always possible to quantify the impacts from the data presented.

Table 15.1. Summary of elephant impacts on vegetation in south-central Africa

Area	**Vegetation type/ plant species**	**Elephant density (head/km^2) [1]**	**Level of impact/ rate of loss**	**Source**
Northern Botswana	Riverine	0.5 (4.6)	high	Sommerlatte 1976
	Baikiaea woodland	1.2	low	Ben-Shahar 1996a
	Mopane woodland	1.2	moderate	Ben-Shahar 1996b
Hwange NP	Bushland	1 (3)	moderate	Conybeare 1991
	Baikiaea woodland	1 (3)	low	Conybeare 1991
	Wooded grassland	1 (3)	moderate	Conybeare 1991
	Terminalia sericea	1 (3)	low	Conybeare 1991
		2.7 (4-5)	6% p.a.	Conybeare (unpubl.)
	Bushland	2.7 (4-5)	high	Conybeare (unpubl.)
	Mopane woodland	1	high	Rogers & Chidziya 1997
Sengwa	Riverine woodland	1	high	Anderson & Walker 1974
	Miombo woodland	1	high	Anderson & Walker 1974
	Mopane woodland	1	high	Anderson & Walker 1974
	Other	1	variable	Anderson & Walker 1974
	Acacia tortilis	<2.9	eliminated	Coulson 1997
	Acacia tortilis	0.7	regeneration	Coulson 1997
Chizarira NP	Miombo woodland	1.5	high	Thomson 1974
	Brachystegia boehmii		18% p.a.	Thomson 1974
Matusadona NP	Miombo woodland	<1	17%-21% p.a.	Robertson 1997
Kruger NP	Various	0.1	generally moderate; locally high	van Wyk & Fairall 1969
Kruger NP	*Aloe marlothii*	0.1	eliminated	Whyte *et al.,* in press
Kruger NP	*Acacia nigrescens*	0.4	30% mortality	Whyte *et al.,* in press
Kruger NP	*Sclerocarya*	0.4 (2.6-5.7)	50% damaged	Jacobs & Biggs 2002b
South Africa	*Sclerocarya*	<0.3	low	Gadd 2002
Luangwa NP	*Colophospermum*	>2	<8% p.a.	Caughley 1976
	Kigelia-Combretum woodland	>2	4% p.a.	Caughley 1976
	Colophospermum coppice	1.1	0.5% p.a.	Lewis 1991
Ruaha NP	*Commiphora ugogensis* woodland	2.4 (4.6)	17% p.a.	Barnes 1983b
	Faidherbia albida	2.4 (4.6)	high	Barnes 1983b
			av. 15% p.a.	
Ruaha NP	Baobab	2.4 (4.6)	3% p.a.	Barnes 1983b
Zambezi Valley	Baobab	2	7.5% p.a.	Swanepoel 1993
Kruger NP	Baobab	0.4	high	Whyte 2001

[1] Overall elephant density is shown with dry season density in brackets.

Northern Botswana has a very large elephant range of about 80,000 km^2, including the Okavango Delta and Chobe National Park, which is contiguous with elephant range in Zimbabwe, the Caprivi Strip and southern Angola. Average annual rainfall is about 700 mm in the north-east decreasing to 450 mm at Maun in the south-west (Sommerlatte 1976). The number of elephants in Chobe has increased steadily from none or very low numbers before about 1945 (Child 1968) to around 80,000 in 1998 (Gibson *et al*., in Chafota 2000) and 120,000 in 2002 (Hoare, Chapter 14). In the wet season, when surface water is abundant, they are distributed widely, but during the dry season they concentrate at a few permanent water sources.

In an ecological survey of north-eastern Botswana, Child (1968) first drew attention to the destruction of riverine vegetation along the Chobe River by elephant. This survey was followed by Sommerlatte (1976), who found that between 33% and 81% of the trees were dead as a result of elephants in four vegetation types. The highest mortality was in *Acacia* woodlands close to the Chobe River. Dry season elephant density at the time was estimated from aerial surveys to be 0.5 per km^2 with a much higher density of 4.6 per km^2 in the stratum close to the Chobe River. Wildfires were also frequent, but were not considered to be an important factor in the mortality of mature trees, except where trees had already been uprooted. They were particularly damaging to the shrub layer, including tree regeneration, and had burnt between 21 and 80% of the shrubs to ground level in the four vegetation types. It was predicted that all adult *Acacia nigrescens* and *Acacia erioloba* trees would be eliminated in 11-23 years (1986-1998), and that ultimately all the trees in the four vegetation types would disappear.

By 1991, dry season elephant densities along the Linyanti River were up to12 per km^2, and although the relative importance of *A. erioloba* and *A. nigrescens* had declined, the trees were still present (Wackernagel 1993). Five heavily utilised species common in 1974 had declined in importance and there were two new species recorded. On the Chobe River virtually all the large *Acacia* trees had gone by 1991, as predicted by Sommerlatte (1976), and much of the former riverine woodland had become *Capparis-Croton* shrubland, a vegetation type not distinguished in 1970 (Addy 1993). In a survey of the riverine woodland along the Linyanti/Kwando River system in 1992, 42.5% of all the trees recorded were dead, with *A. erioloba* having the highest proportion of dead trees (67%), followed by *A. nigrescens* with 46% (Coulson 1992). Felling by strong winds was found to be an important cause of tree mortality and it was thought that elephant damage predisposed trees to damage from other factors. Coulson (1992) also noted that, although baobab trees were not found in the riverine woodlands, all those seen during the survey were severely damaged by elephants.

Vegetation change in northern Chobe NP was assessed from aerial photos in 1965, 1985 and 1998 (Mosugelo *et al.*, in press). The study area covered 15 km on the south bank of the Chobe River and extended to about 10 km away. Aerial photo interpretation was supported by ground work in the three main vegetation types - shrubland, mixed woodland and woodland - to assess vegetation cover and the impact of browsing and fire. The area of woodland declined from 60% of the study area to 30% between 1962 and 1998, the area of mixed woodland increased from 19 to 34%, and the area of shrubland increased from 5 to 33%. The rate of change appeared to be greater from 1985 to 1998 than from 1962 to 1985 and was most marked closer to the river. In 1962, woodland was the dominant vegetation type between 2 and 4 km from the river, but by 1998 it was not dominant closer than 8 km, and had totally disappeared within 2 km of the river. It is not clear which species were lost as *Baikiaea plurijuga* is the dominant species in both woodland types and is not much eaten by elephants. It is possible that suppression of other species by browsing led to an increase in the amount of grass and fire as more than 50% of the trees within 7 km of the river had fire scars. Recruitment of trees could then have been prevented by a combination of fire, browsing by smaller herbivores and trampling. The proportion of plants with fire scars increased linearly with distance from the river, but fire was no longer considered an important factor in shrubland and mixed woodland close to the river, whereas browsing was. Utilisation of browse by elephants was measured on three species combined, *Combretum apiculatum, C. elaeagnoides* and *C. mossambicense,* and declined linearly away from the river. The riparian fringe woodland was not sampled on the ground, but by 1998 only small fragments remained from a continuous strip in 1962.

The *Acacia* and riverine woodlands of Chobe NP and Moremi Game Reserve were also sampled from aerial photographs (EcoSurv 1991). In *Acacia* woodlands, canopy cover decreased from 46.5% in 1951 to 8% in 1985 in Chobe, and from 46.5% to 20.7% in 1983 in Moremi. In the Savuti area of Chobe NP regeneration of *A. erioloba* was investigated and found to be inhibited by elephants, small ungulates and fire (Barnes 2001). In average rainfall years, no new seedlings survived.

Ben-Shahar (1993) recorded vegetation damage from elephants and other factors at 33 sites in six vegetation types across northern Botswana, but it is not clear whether the data were recorded from all plants in the plots or those of the dominant species only. He concluded that:

- there was a high variation in the proportion of woody plants damaged by elephants, particularly near permanent water sources,
- the percentage of important food plants damaged increased significantly with proximity to temporary water sources, and
- there was a clear distinction between the effects of elephants and fire on different species.

Ordination suggested three zones of elephant and fire impact, (a) high fire and low elephant impact, (b) high elephant and low fire impact, and (c) low elephant and low fire impact. He found no correlation between biomass of vegetation removed by elephants and elephant density from aerial surveys.

Regressions and multi-variate analysis were used on similar data from 32 sites in three vegetation types by Ben-Shahar (1996a). The vegetation types were dominated by *Acacia erioloba, Baikiaea plurijuga* (teak) and *Colophospermum mopane* (mopane), respectively. He concluded that *C. mopane* was susceptible to elephant damage, while *B. plurijuga* was more prone to fire damage, and that with frequent fire, *B. plurijuga* density would decline even at low elephant density. Using mean values of elephant and fire effects derived from the data, the model predicted that tree density would decline in teak woodland and mopane woodland only when elephant densities exceeded 9 per km^2 and 11 per km^2 respectively. At these mean levels of elephant browsing and fire frequency, no loss of trees was predicted in *A. erioloba* woodland, which is surprising given the reported declines in this species elsewhere in Chobe (Sommerlatte 1976, EcoSurv 1991, Coulson 1992). He concluded that potential decline of woodlands from elephant browsing was probably confined to those dominated by plants that are principal food sources, e.g. mopane. What appear to be the same data for the mopane sites alone were analysed in more detail (Ben-Shahar 1996b). Regression models were used to relate vegetation biomass to elephant density and rainfall. These predicted that even at elephant densities of 15 per km^2 over-utilisation would only occur if plant growth was less than 70% of maximum potential. He concluded that on a regional scale there was no evidence that elephants would reduce the biomass of mopane woodlands below a sustainable level, even if elephant density increased considerably beyond the prevailing level. At that time the elephant population of the 80,000 km^2 elephant range of northern Botswana was estimated to be between 65,000 and 94,000 (0.8 per km^2 and 1.2 per km^2), but around water at the end of the dry season was estimated to be 7-10 per km^2.

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Ben-Shahar (1998) also used similar techniques to compare plant densities of the dominant species in the three same vegetation types as before in 1992, 1993 and 1995. The plot boundaries did not coincide exactly in each year but the data indicated that in *Baikiaea* woodland the density of trees above 10 m tall declined between 1992 and 1995. In all three vegetation types the density of trees between 3 m and 10 m tall declined from 1992 to 1993, but increased again from 1993-1995. No explanation was offered for this and he concluded that elephant were not causing a decline in the woodlands, but that fire damage was high, especially in *Baikiaea* woodland.

Also working in an area of Kalahari sand vegetation, Conybeare (1991) monitored elephant occupancy and changes to the woody vegetation in three vegetation types in Hwange National Park, Zimbabwe from 1980 to 1985. Long-term average annual rainfall in this study area is about 630 mm, approximately the same as Chobe NP. Permanent plots were sited at increasing distance from artificial water points in *Baikiaea plurijuga* woodland, *Terminalia-Combretum* bushland and *Acacia-Eragrostis* wooded grassland. Overall elephant density in the Park was about 1.2 per km^2, and dry season densities in the study area were about 3 per km^2 in the 1980-1985 study period. Trees were considered to be woody plants over 3 m in height with a stem diameter of 6 cm or greater, while plants that met these criteria, but had been reduced in height below 3 m by some form of damage were classified as "trees converted to shrubs" (Anderson & Walker 1974). Converted trees were often able to grow back into the tree layer. Tree density in these plots was recorded again in 1992 and 2002 (Conybeare, unpublished data). Elephant density within the study area was not monitored specifically after 1984 so it is not possible to link later changes to trends in elephant density in the study area. However, in the Park as a whole, elephant density increased again after the end of culling in the mid-1980s. If dry season density within the study area increased by the same proportion, in 1992 density was 4.4 per km^2 and 5.1 per km^2 in 1999.

During the study, species diversity of trees and shrubs measured by the Shannon-Weiner function (Poole 1974) dropped on 15 out of 20 plots between 1980 and 1984, while species richness declined on nine, primarily from the loss of shrub species that previously occurred at low density.

In 1980 in bushland, the vegetation type with the highest elephant occupancy, 21% of the total potential tree population was converted to shrubs by breakage to below 3 m height. During the study elephants killed annually on average 3% of the trees and converted 10% to shrubs. Tree density had declined by 11% in 1985 and by 26% in 2002, when 32% of the trees were converted to shrubs. The dominant tree, *Terminalia sericea*, had not changed in density by 1992, but by 2002 had declined by 62%. Meanwhile, density of a species rarely damaged by elephants, *Ochna pulchra,* increased from 9 to 129 trees per ha by 2002 to become the most abundant tree. Another little-damaged species, *Lonchocarpus nelsii,* increased in density from 3 to 29 trees per ha. The effects of elephants were to change species dominance and reduce tree density and average tree height.

In *Baikiaea* woodland, where *B. plurijuga* was little damaged by elephants, 11% of the potential trees were in the shrub category in 1980. On all plots, elephants killed 1% of the mean tree population per year and converted 3% to shrubs. Tree density had declined by 11% in 1985 when 14% were converted, but by 2002 there had been a slight increase in tree density and a reduction in the proportion of converted trees to 7% of the population. Density of *Lonchocarpus nelsii* increased by 31%, while some species at low density in 1980 declined in density. Elephants did not appear to have a great impact on the physiognomic structure of this woodland but did alter some species importance rankings.

In wooded grassland, the vegetation type surrounding pans, all three plots were within 1.6 km of a permanent water point. In 1980, 57% of the tree population was converted, rising to 64% in 1985. Elephants killed on average 2% of the tree population per year and converted 10% to shrubs. Tree density had declined by 34% in five years. By 1992, however, this trend had been reversed and tree density had increased by 26% since 1980, and a smaller proportion (38%) of the total tree population was converted to shrubs. There had however, been a change to species importance rankings. The most abundant trees prior to 1980, *Terminalia sericea* and *Combretum collinum*, were replaced by *Dichrostachys cinerea* and *Combretum hereroense* and now ranked third and fourth in abundance. There are no later data for wooded grassland as not all the plot boundaries could be located accurately in 2002.

In all three vegetation types, a higher percentage of converted than unconverted trees died from causes other than elephants and frost, suggesting that elephant damaged trees were more likely to die from other causes than undamaged trees. In summary, the declines in tree density that took place between 1980 and 1985 only continued in bushland, while in woodland and wooded grassland there was some recovery of physiognomic structure with altered floristic composition.

The increase in woody cover in woodland and wooded grassland found in this study was supported by a wider study of aerial photographs of Hwange NP, taken between 1959 and 1994 (Rogers & Chidziya 1997). There was no change, or a slight increase, in canopy cover in *Baikiaea* woodland with a low frequency of fire, but some reduction where fire was more frequent. Canopy cover increased in bushed grassland and grassland, while it declined in riverine woodland and in mopane woodland, most of which was within 10 km of permanent water. Most of the mopane woodland canopy was gone by 1983.

A considerable amount of work on elephant impacts has been carried out in the Sengwa Wildlife Research Area (SWRA), situated at the southern edge of Chirisa Safari Area in central Zimbabwe with an average annual rainfall of about 640 mm. The area is 373 km^2 in extent and elephant density remained below 1.5 per km^2 until the late 1970s, then increased to about 2.9 per km^2 by 1981. Aerial photographs of the area showed very little change in woodlands between 1951 and 1965, but a marked change after 1965 (Cumming 1981a). Anderson and Walker (1974) studied woody vegetation composition and elephant damage in the three major vegetation types and seven minor types when elephant density was about 1 per km^2. In mopane woodland, the vegetation type with the largest area, 22% of trees of the most important five species were dead and 45% had been converted to shrubs (<3 m tall). In miombo woodland, 27% of the trees of the most important 10 species were dead and 33% had been converted to shrubs, while in *Acacia - Grewia* riverine woodland 48% of the 10 most important tree species were dead and 12% had been converted to shrubs. The upper canopy layer of this riverine community had formerly been dominated by *Acacia tortilis*, which was now placed fourth with 87% of the trees dead. The shrub layer had formerly been dominated by *Grewia flavescens*, but this was reduced to minor importance by elephant damage. The impact of elephants was strongly linked to preferred food species. In *Baikiaea-Baphia* communities, where *Baikiaea* the dominant tree was not utilised, total elephant damage to trees was low (7%), compared to 40% for miombo woodland and 34% for the entire study area. In this community, elephant impact was more noticeable on the shrub component. These ratings did not include bark damage, which was assessed separately; the most affected species being *Brachystegia boehmii, Acacia tortilis* and *A. nigrescens*. In order to preserve the vegetation types of the SWRA, an initial reduction of elephant numbers to about 40% of the existing population density was recommended (0.4 per km^2), but no culling was done until much later.

Guy (1981) remeasured the plots in the three major vegetation types in 1976. Total tree and shrub biomass had declined further in miombo and mopane woodlands by 45% and 6%, respectively. Elephants were considered to be the main cause of the decline, but fire was probably also a factor. In the riverine woodland formerly dominated by *A. tortilis* biomass had increased by 14% from recruitment of both shrubs and trees but of species other than *A. tortilis*, while in *Faidherbia albida*-dominated riverine woodland there was little change. Coppice growth led to more browse in the lower levels than formerly, except in the *F. albida* riverine community. Culling of elephants at Sengwa started in 1978 but an effective reduction in numbers was only achieved by 1983/84 when elephant density was reduced to about 0.7 per km^{2}, after which there was some recruitment of *A. tortilis* trees (Coulson 1997).

Guy (1989) compared miombo woodland inside and outside the SWRA in 1985, after elephant density had been reduced. The boundary was fenced at this point and elephants were actively discouraged from entering the Communal Lands outside, so that the woodland inside was affected by elephants and fire while that outside had fire but little impact of elephant. The outside woodland was considered to be typical of miombo in this area as, although biomass was estimated to be reduced by about 35% largely as a result of fire, there was little change in the importance of individual species. Inside the SWRA tree density was lower, stem area and biomass were 67% lower, and species importance values and ranks had been much changed because of a reduction in species preferred by elephants; the previously dominant species *Brachystegia boehmii* had virtually disappeared from the canopy layer. Shrub density and biomass were higher inside the SWRA, but individual shrubs inside were on average smaller and there was some change to species rankings. The result was an open woodland dominated by species not attractive to elephants and a relatively dense shrub layer of fire-resistant species. It was concluded that the reduction in the number of elephants to 250 (0.7 per km^2) was allowing some regeneration of the miombo woodland.

Mapaure (2001) investigated miombo woodland in the SWRA in 1998, by which time there were again in excess of 1000 elephants (>2.6 per km^2). In comparison to 1972, the time of Anderson and Walker's (1974) study, the density of large trees was 65% lower, while the density of small trees and shrubs had increased. The heavily damaged tree *B. boehmii* had been almost eliminated and the two most important species were *Julbernardia globiflora* and *Pseudolachnostylis maprouneifolia*. A number of shrub species had declined in density, while others had either increased or appeared, so that where woody cover was increasing again, the species were not typical miombo dominants but Combretaceae, leading to development of woodland thickets. It was found that elephant use of the miombo habitat was lower than previously; preferred species had declined in abundance and the elephants appeared to make more use of other habitats rather than switch to different species within the miombo. It was also found that elephant damage to the miombo vegetation was higher close to a boundary with other favoured habitats such as riverine and mopane woodlands than close to the less-used habitat of *Julbernardia-Xerophyta* wooded bushland. Elephant impact was therefore not necessarily uniform across the full extent of a particular vegetation type. Mapaure also analysed aerial photos taken between 1958 and 1996 for change in woody cover in the miombo woodlands of the SWRA. There was a steady decline in woody cover from 1958 to 1983, as was reported by Cumming (1981a) for the area as a whole, followed by a slight but insignificant rise to 1996. Overall, there was a significant decline of woody cover between 1958 and 1996 of 28.4%, from 95.2% to 68.2%, an average of 0.75% p.a., although there was a wide range of percentage changes between years.

Chizarira National Park, situated in northwest Zimbabwe on the edge of the central plateau, is 1910 km^2 in extent and overlooks the Zambezi valley, from which it is separated by a steep escarpment (Thomson 1975). The Park shares a short common boundary with Chirisa Safari

Area, and some elephant movement between Chizarira and SWRA certainly occurs. The vegetation of the plateau area was a mixed species deciduous wooded grassland, with a central ridge of *Brachystegia boehmii* woodland covering about 10% of the park. Elephant were able to move in and out of the park; numbers were higher during the dry season. Regular aerial sample counts were carried out after 1968 and although the technique did not yield reliable density estimates, it appeared that elephant numbers were increasing. Elephant damage to *B. boehmii* trees by bark removal, removal of branches, breakage of stems and uprooting was first noted in the mid-1960s and trees were sampled in a variety of ways on the central ridge in 1971, 1972 and 1973 (Thomson 1975). During the study, the percentage of undamaged trees decreased, the percentage in all damage categories increased, and elephants killed trees at a rate of 18% per year. As annual fires burnt any regenerating saplings and prevented recruitment into mature size classes, it was predicted that the woodland would be eliminated in 6 years and that is what happened, in spite of attempted fire control and the culling of 400 elephants (Cumming 1981b).

Matusadona National Park in Zimbabwe is situated on the shores of Lake Kariba and is divisible into a valley area and a plateau area of miombo woodland in the Zambezi escarpment. In a study of aerial photographs taken between 1959 and 1981, Robertson (1997) found that canopy cover on the plateau declined by 17 to 21% per year on shallow and moderate slopes between 1959 and 1973, while the rate of change on steeper slopes was more variable. Canopy cover was reduced from 60% in 1959 to 2% in 1973 in the part of the plateau with year-round elephant occupancy at a time when elephant density was below 1 elephant per km^2. In that part of the plateau where elephants move out of the park for part of the year, the loss of canopy cover took place more slowly, but canopy was reduced to 10% by 1973.

Kasungu National Park in Malawi, with higher rainfall of 780 mm per year, covers 2316 km^2 and holds about 1000 elephants, concentrated in the central area making density higher there than the overall park density (Jachmann & Bell 1985). The effect of elephants was to modify miombo woodland to a short coppice phase, that was then maintained by elephant browsing.

In a general study of biodiversity with and without elephants in miombo woodland in Zimbabwe in 1994, Cumming *et al*. (1997) compared woody plant density, cover and species richness between elephant impacted sites that had sustained elephant densities in excess of 1 per km^2 for 20 years and intact sites that had very low occupancy. Some sites were separated by a fence and some by a gorge impassable to elephants. The density of large trees, woody cover and tree species richness were significantly higher in intact than impacted sites, while the density and cover of shrubs was significantly lower in intact sites. The mean number of species of tree size (>3 metres height) was 25.5 per site in intact woodland compared to 11.2 in impacted woodland.

The Luangwa Valley in Zambia supported a very large elephant population, probably in excess of 100,000 animals at a density of more than 2 per km^2 in the early 1970s (Caughley & Goddard 1975). In a study done in and around South Luangwa National Park, Caughley (1976) found that in *Colophospermum mopane* (mopane) woodland elephants felled 138 trees per km^2 per year (4% of the standing crop), and estimated that as many or more were killed by ring-barking. The effect of elephants was to change the structure of stands from a spread of sizes to a double-tiered form, the lower tier of coppice around 2 m high and an upper tier of trees over 8 m. When trees in the upper tier were felled by elephants they were not replaced, so elephants prevented recruitment rather than regeneration. As seeds were only produced by large trees their removal also reduced the seedbank. In a *Kigelia-Combretum* woodland on alluvial soils in the same area, elephants felled 4% of the trees of over 20 cm girth in one year. They damaged 6% by pushing them more than 30 degrees from vertical, which caused root damage, and browsed 24% in excess of annual production, by removal of branches. In summary, elephants were killing mopane much faster than recruitment could take place into mature size classes, and converted woodland to grassland in some sites. In *Kigelia-Combretum* woodland there was also a trend to more grassland.

Lewis (1991) also worked in the South Luangwa but concentrated on factors that affected elephant damage and the reasons for differences in woodland physiognomy, giving little direct impact data. He found that differences in mopane woodland composed primarily of adult trees and mostly coppice could be attributed to different soil types, but his results also supported Caughley (1976) that browsing by elephants promoted coppice formation in *C. mopane*. Coppiced trees were able to sustain heavy browsing with a low mortality rate of 0.5% per year at an elephant density of about 1.1 per km^2. He hypothesised that soils with a high nutrient status in the A-horizon allowed coppice to persist in spite of heavy browsing, but that periodic die-offs of trees could occur, perhaps associated with depletion of soil nutrient levels or drought. At one site outside the main study area, where elephant density was particularly high owing to proximity to a lodge and some protection from poaching, coppice died after a season with 14% lower than average rainfall. Mopane woodland on islands in Lake Kariba was also converted to bushland and maintained as coppice < 1 m high by elephants that were able to move between the islands and the mainland (Mapaure & Mhlanga 2000). Elephant density could not be determined because of this movement, but there had been no fire for some time and the vegetation structure appeared to be stable. The authors hypothesised that frequent fires would weaken smaller plants and cause a slow regression to a fire-climax grassland, while a reduction in elephant density would allow gradual redevelopment of woodland.

One of the first studies on elephant impacts in southern Africa was done in Kruger National Park, South Africa (van Wyk & Fairall 1969). At the time overall elephant density was low at 0.13 elephants per km^2 and utilisation of the vegetation was found to be generally low to moderate, although *Aloe marlothii* had been almost completely eradicated locally 10 years earlier (Whyte *et al.,* in press). Only in a few small areas were impacts severe and these were in dry season concentration areas near permanent water. Utilisation of small trees and shrubs was negligible and elephants fed mostly from large shrubs. Utilisation of trees was higher where shrub density was low or shrubs had been removed temporarily, e.g. by fire. Some species were relatively heavily used and in later years the loss of marula (*Sclerocarya birrea*) and knobthorn (*Acacia nigrescens)* became a cause of concern (Whyte *et al*., in press). In 1978, when elephant density was 0.4 per km^2, up to 6.5% of the *Sclerocarya* in a sample near roads were ringbarked or felled in one season (Coetzee *et al*. 1979). At that time, damage was thought to be localised and not a threat to the general population of *Sclerocarya*, but later work showed that they had been completely lost from one habitat and were severely damaged in others (Jacobs & Biggs 2002a, 2002b). In another survey in the late 1970s, 64% of the sampled *A. nigrescens* were found to be damaged with almost 30% dead or dying (Whyte *et al*., in press).

Trollope *et al.* (1998) studied the change in woody plant cover in the four major vegetation types in the Kruger National Park using aerial photographs, two on sandy soils and two on clay soils. They concluded that between 1940 and 1960 there was negligible change to the density of large trees on the sandy soil types and a moderate decline on clay soils. Between 1960 and 1986/89 there was a moderate decline on the sandy soils and a moderate to marked decline on clay soils. It was thought that elephants reduced the density of large trees, and a combination of elephants and fire prevented regeneration. Changes in woody vegetation did not reduce species diversity but altered structure leading to a short woodland (bushland) with a low density of large trees. Using herbivore exclosure plots in three vegetation types, it was found that although the density of shrubs was lower outside than inside, the differences were not significant. Phytomass was however, significantly lower outside than inside the plots at the two drier sites and there was a higher proportion of large shrubs inside than outside, indicating that elephants were having some impact on shrub density and biomass.

In Sabi Sand Game Reserve, bordering Kruger National Park, elephants were to a large extent excluded by a fence from 1961 to 1993. When the fence was removed elephants started to enter the Reserve, primarily during the dry season (Hiscocks 1999). By 1998 (5 years) up to 29% of some species were dead as a result of elephant damage.

Ruaha National Park in south-central Tanzania is 10,300 km^2 in extent. With adjacent game reserves it forms a 25,000 km^2 area that was first given protection early in the 1900s (Barnes 1983a). It lies on the ecotone between the miombo woodlands of south and west Tanzania and the *Acacia* and *Commiphora* woodlands and bushlands of north and east Tanzania. Serious tree damage in parts of the park was reported soon after the it was proclaimed in 1964 (Savidge 1968), and an aerial survey in 1977 showed that tree loss was evident all over the park at a time when elephant density was 2.4 per km^2 (Barnes & Douglas-Hamilton 1982). Part of the area falls into a section of rift valley where the average annual rainfall is 580 mm. Dry season elephant density was estimated to be 4.6 per km^2 when Barnes (1980, 1983b) investigated the effects of elephants on three tree species between 1976 and 1982. *Commiphora ugogensis* was an important component of the woodland in the area, *Faidherbia albida* occurred on alluvial soils along the Great Ruaha river and baobabs (*Adansonia digitata)* were particularly plentiful. In 1976/77 there was serious damage to all three species. The density of *C. ugogensis* outside the Park was about 250 trees per ha, but inside the park had been reduced to 4% of this. Elephants were killing 17% of the trees annually and by 1982, *C. ugogensis* had been completely eliminated in places. Between 1977 and 1982 the density of live *F. albida* had declined by 72% in one stratum and 84% in the second. The density of baobabs had decreased by 45% and there were no small trees. The final outcome of this level of impact was not seen because poachers killed around 60% of the elephants in the Park between 1977 and 1984. The patterns of mortality found here are discussed further in section 15.3.1.

The impact of elephants on baobabs was also studied in Kruger NP by Whyte (2001) in two areas with different histories of elephant occupancy. Where elephants had been present for longest, a significantly higher proportion of the trees showed severe damage; smaller size classes were poorly represented in comparison to an area which elephants had occupied more recently. At a control site with no elephant, small size classes formed a higher proportion of the population than at either of the sites with elephants. Actual mortality was highest during a period of low rainfall between 1981 and 1994, suggesting that damaged trees were more liable to die from other stress factors. These impacts occurred even at relatively low elephant densities.

At a higher elephant density of about 2 per km^2 in the Zambezi Valley in Zimbabwe, in a sample of 124 trees, 99% sustained damage over a 4 year period and 29% were killed (Swanepoel 1993). Annual mortality was 7.5%, considerably higher than the 3% recorded at Ruaha with higher elephant density (Barnes 1983b).

15.2.2 Impacts on the Herbaceous Layer

Elephants may feed on significant amounts of grass at some times of year. At Sengwa, more than 30% of feeding time was spent grazing in the early wet season (Guy 1978), while in Ruaha NP, more than 60% of the diet in the wet season was grass (Barnes 1982). If green grass is available in the dry season it will be eaten. On floodplain grasslands in Luangwa, elephants spent 40% of total feeding time during the day grazing in the early dry season and 21% in late dry season (Lewis 1986). They pulled up tussocks and ate the basal parts, including roots of *Andropogon* and *Hyparrhenia* spp. and also *Setaria eylesii,* with much of the leaf and stem being discarded

(Lewis 1987). In habitats other than the floodplain, tall grasses were also eaten extensively in the dry season, especially in the early parts when patches of grass could still be found in the woodlands.

In spite of this, the impact of elephant on the herbaceous layer has been considered to be insignificant as grasses are able to regenerate rapidly in the wet season when most elephant grazing occurs (Owen-Smith 1988). However, grasses are at their most vulnerable at this time, when defoliation weakens the plant, not in the dry season when the plants are generally dormant. The importance of elephants as grazers, particularly when they occur at high densities, may have been underestimated.

Changes to the herbaceous layer following the provision of artificial water have been well documented, but the role of elephants in contributing to these changes has never been investigated (Thrash *et al*. 1991).

15.3 FACTORS AFFECTING ELEPHANT IMPACT ON VEGETATION

15.3.1 Vegetation Type and Geographic Area

It might be expected that the species composition of vegetation would be a factor affecting the levels of impact since not all plant species are equally palatable. Palatability is affected by the chemical composition (nutrient level and secondary compounds) and mechanical properties of the plant part (Jachmann & Bell 1985). In the SWRA in Zimbabwe, Guy (1976) found that the majority of plants were eaten in proportion to their occurrence, while some species were selected and others were avoided. Stokke and du Toit (2000) found that in Chobe NP elephants showed some selection for feeding sites and that family units fed in areas with more species than did adult males. In the same area, Chafota (2000) found that relatively few of the available species were actually used, the greatest number being in the hot dry season. These two studies seem to indicate a greater degree of selection than was found by Guy (1976).

As a result of this species selection by elephants, the degree of damage to vegetation will differ between vegetation types in close proximity to each other and within the same vegetation type depending on the pattern of species distribution. Plant species distribution within a particular vegetation type may be affected by minor undulations in the ground surface; this feature, termed the 'terrain ruggedness index' by Nelleman *et al.* (2002), may also affect the pattern of elephant utilisation.

Since elephants show preference in their feeding behaviour, the level of utilisation of a particular species at any one locality is likely to be affected by what other species are available. It may be different in different localities or at different times. In Chobe NP, Stokke (1999) found no selection for *Burkea africana*, and in Kasungu NP, Malawi, selectivity was low (Jachmann & Bell 1985). However, a high level of damage was recorded in Hwange (Conybeare 1991) and Sengwa (Anderson & Walker 1974). In Chobe, *Bauhinia petersiana* was utilised less than expected in one study (Stokke 1999), but found to be favoured in another (Chafota 2000). *Pseudolachnostylis maprouneifolia* was heavily used at times in Kruger (van Wyk & Fairall 1969), but not favoured at Sengwa (Anderson & Walker 1974, Mapaure 2001) or in Chobe (Stokke 1999).

There have been a number of studies investigating the relationship between plant nutrient concentration and utilisation by elephants. In Kasungu NP, mature foliage selected by elephants in miombo woodland was characterised by a high mineral and sugar content while those species avoided were high in secondary compounds and often in lignin (Jachmann 1989). Immature leaves were generally rejected, probably because of the high content of secondary compounds. Protein content of the foliage did not appear to be important, perhaps because protein was available in sufficient amounts throughout the year, although earlier work in the same area had showed a significant correlation between utilization and the protein and sodium content of foliage (Jachmann & Bell 1985). It was also suggested that selective felling of trees could be related to varying concentrations of polyphenols in mature and coppice phase trees under the influence of browsing.

Hiscocks (1999), working at Sabi Sand Game Reserve in South Africa, analysed the cambium layer of eight species in three categories of bark damage, preferred species, less preferred and rarely damaged. The preferred species had higher levels of nitrogen, sodium and magnesium than those in other categories.

On the other hand, Thomson (1975) analysed the bark of five tree species in Zimbabwe but could not find significant differences in mineral or crude protein content between species of different apparent preference. Anderson and Walker (1974), also in Zimbabwe, analysed the bark and leaves of 16 plant species for percentage calcium, magnesium, sodium, potassium, total salts and crude protein but could find no significant relationship between elephant damage and any of the chemical constituents. Soil samples were analysed for a number of soil factors but the only significant correlation with elephant damage was for sodium in the mopane woodland transects. Working in the same area, Dudley (1999) was unable to confirm a higher intensity of browsing linked to sodium-rich soil as separating these factors was confounded by probable coincidental relationships. The nitrogen content of mature mopane leaves was significantly higher in plots adjacent to the Sengwa River, as was soil sodium, so that the higher browsing intensity found there could be attributed to proximity to water. He also found that sodium and calcium concentrations varied greatly between soil samples taken in close proximity to each other.

In Kalahari sand woodland adjacent to Hwange NP, Holdo (2003) found that elephant use was positively correlated with leaf calcium, magnesium, potasium and protein, but not sodium, phosphorus or fibre. The absence of apparent selection for sodium found in other studies (Jachmann & Bell 1985), was explained by the presence of sodium in soil licks at far higher concentrations than are found in plant tissues. The importance of soil sodium to elephants in this area has been recorded previously (Weir 1972, Holdo *et al*. 2002).

Elephant feeding behaviour appears to vary between species in other ways, leading to different patterns of mortality in relation to tree density (Barnes 1983b). Barnes found that with *Faidherbia albida* the proportion of the tree population killed correlated with tree density, so that when tree density became low, the proportion killed also declined. With *Commiphora ugogensis,* although the number of trees killed was positively correlated with tree density the proportion was not, so that high numbers of trees continued to be killed, even when the trees had reached a low density. A third pattern of mortality was shown by the baobab *Adansonia digitata* where a fixed number of trees were killed annually regardless of tree density, a pattern that would lead rapidly to local extinction of the tree population, as was thought to have happened at Tsavo (Leuthold 1977). A fourth pattern of mortality was possible, where the level of utilisation was higher at low tree density, which was suggested for *Acacia xanthophlea* at Amboseli (Western & Van Praet 1973). These different patterns of tree mortality can influence the rate of decline of a heavily used species.

15.3.2 Elephant Density

There is a clear link between elephant density and damage to vegetation. In the Luangwa Valley in Zambia, Caughley (1976) found through regression analysis that the number of *C. mopane* trees felled was 14 times more dependent on elephant density than on tree density. Apart from this general trend however, it is difficult to be very specific about levels of damage at particular elephant densities because of the other factors that affect elephant impact, but it is likely that the relationship between elephant density and damage is exponential (Anderson & Walker 1974).

Establishment of the relationship between elephant density and vegetation damage is made more difficult by the different scales at which measurement of the two variables takes place. Elephant densities are usually measured on a Park-wide basis, sometimes with attempts to apportion different densities to different vegetation types on the basis of occupancy (Conybeare 1991), while impacts are usually measured in much smaller areas.

Anderson and Walker (1974) attempted to relate total elephant damage in different vegetation types to elephant density in them, as obtained from monthly game-count transects. There was no close relationship and it is probable that average densities derived from counts done in the morning only were not representative of overall elephant occupancy. Also elephant occupancy at that time may not have been related directly to time spent feeding. Nevertheless, at an elephant density of about 1 per km^2 at Sengwa the impact of elephant on vegetation was severe and continued to increase as elephant density increased further to 2.9 per km^2. When elephant numbers were reduced to a density of around 0.7 per km^2 in the early 1980s, it was soon obvious that regeneration and recruitment of *Acacia tortilis* in the riverine community was taking place (Coulson 1997). In 1982 there were no remaining *A. tortilis* trees in the canopy layer and very few in the tree layer (>3 m tall). By 1986, there were 15-20 trees per ha, of which a few trees (<5 per ha) had reached canopy size. From these data it was estimated that to maintain a canopy tree density of 25 trees per ha, elephant density would have to remain below 0.25 per km^2. There was also some recovery of the vegetation in the form of tree regeneration in other vegetation types following the reduction in the number of elephants (Guy 1989, Mapaure 2001).

In Kruger NP, utilisation was considered to be generally low to moderate at an overall density of 0.13 elephants per km^2. Because of concentrations in the dry season, density reached 0.24 per km^2 in some areas. In areas close to permanent water and often areas of riverine vegetation, 32% of adult trees and 41% of large shrubs were found to be utilised (van Wyk & Fairall 1969). A positive correlation was found between elephant biomass and the level of utilisation of trees and large shrubs. As a result a maximum elephant density of 0.29 per km^2 (0.75 per square mile) was recommended to avoid total destruction of vulnerable areas near water. Elephant numbers did in fact increase to almost 9000 in 1970 before it was reduced by culling and held at around 7500 (0.4 per km^2) until 1994. Controlling elephant density at this level did not prevent conspicuous damage to vegetation in places, especially during a low rainfall year (Coetzee *et al*. 1979, Whyte *et al.*, in press). Damage to *Sclerocarya* trees has been a particular concern in Kruger NP. An investigation in three landscape units with estimated elephant densities between 2.6 per km^2 and 5.7 per km^2 showed that almost half the surveyed population of marula suffered from elephant damage, predominantly bark stripping and felling (Jacobs & Biggs 2002b). This species was also surveyed in three other Reserves in South Africa with low elephant densities of 0.08-0.3 per km^2. Impacts were thought to be sustainable since tree mortality rates were low, with affected trees often recovering and small trees were not preferentially targeted (Gadd 2002).

In a review of elephant impacts on *Brachystegia* woodland in Zimbabwe, Robertson (1993) found that, with a few localised exceptions, woodland did not survive where elephant density exceeded 0.5 per km^2. On the basis of other evidence, she suggested that even at a density of 0.2 elephants per km^2, tree density may decline in *Brachystegia* woodland.

15.3.3 Elephant Sex and Age Class

Most uprooting of trees is done by adult male elephants. Guy (1976) studied feeding of elephants in the SWRA by following individual animals of both sexes. Of the males under observation, 78% pushed over trees compared to 39% of females. Hiscocks (1999) observed that of 97 trees uprooted, adult males were responsible for 91 (94%). Feeding behaviour differences were also found between adult males and other categories in northern Botswana (Chafota 2000, Stokke & du Toit 2000) and in Ruaha (Barnes 1982). Adult males fed from fewer plant species than did family groups but ate a bigger range of plant parts and fed for longer at each plant, thereby probably causing more damage to individual plants. Adult males broke more and bigger branches, ate more roots and felled more and larger trees than family units. Most feeding for all categories was however, lower than 2 m above the ground. Both males and family units used most woody plant species in proportion to their availability, with only a few species being used proportionally more or less.

Based on measurements between 1976 and 1982, Barnes (1980, 1983b) predicted the elimination of baobabs in a section of Ruaha NP. In 1989 there had however been little change to baobab numbers in spite of relatively high elephant densities, probably because virtually all the adult males had been killed by poachers (Barnes *et al.* 1994), supporting the observation that males are primarily responsible for killing baobabs.

15.3.4 Seasonal Factors

Most damage to woody plants occurs in the dry season when elephant distribution is restricted by availability of surface water (van Wyk & Fairall 1969) and woody plant parts make up a bigger proportion of the diet. Elephants use a wider range of species in the dry season, particularly during the hot, dry season and most damage to canopy trees takes place in the dry season (Barnes 1982, Chafota 2000). Hiscocks (1999), working in Sabi Sand Reserve, recorded tree felling throughout the year but said that the number uprooted increased in the dry season. Guy (1976) only recorded tree felling during dry season observations but his wet season observations were at the start of the wet season only and tree felling may have occurred later. Most bark stripping takes place in the dry season, associated with the onset of flowering or leaf production, although some bark may be eaten throughout the year.

15.3.5 Proximity to Permanent Water

Elephant impact on the vegetation is usually higher close to water sources, particularly permanent water (van Wyk & Fairall 1969, Conybeare 1991, Swanepoel 1993; Thrash *et al.* 1991) but also close to seasonal water sources (Ben-Shahar 1993). The introduction of two artificial water points at Savuti in Chobe NP, led to increased damage to vegetation (Barnes, 1999). Tree loss measured from aerial photographs was highest close to water in Gonarezhou NP in southern Zimbabwe (Tafangenyasha 1997).

The combination of palatable plant species, shade and proximity to water found in riverine woodlands has led to this vegetation type being highly impacted (Child 1968, Anderson & Walker 1974). Riverine woodlands are probably the most vulnerable vegetation type to elephant damage. Occupancy by elephants may not be linearly related to distance to water but can be very high in close proximity and then drop to a more uniform level for a distance of some kilometres (Conybeare 1991).

15.3.6 Soil Factors

The high water infiltration rate on deep, light-textured soils favours the growth of woody species. As a result, density and biomass of woody plants are usually higher than on heavier soils and browse removed by elephants is more quickly replaced. Many of the tree species that grow in deep sandy soils are relatively unpalatable to elephants, e.g. *Baikiaea plurijuga* and *Erythrophleum africanum*. This can also reduce the visual impact of elephant browsing. The same species may even respond differently to elephant browsing on nutrient-poor and nutrient-rich soils (Moe *et al.* 2003). In sandy soils, trees are more likely to be pushed over than broken, although the species and it's rooting characteristics also have an influence. The occurrence of natural coppice mopane shrubland that appears to have no potential to develop into woodland has been linked to soil characteristics (Lewis 1991).

Bell (1981) argued that elephant impacts on vegetation would be most severe in conditions of high soil nutrients and high infiltration rates. Such areas could be characterised as having the potential for many trees and many elephants, e.g. Luangwa valley, Zambia and the coastal plain of Natal, South Africa. In this model, miombo and Kalahari sand woodlands, with high infiltration rates and low nutrient status, would fall into the category of many trees and low elephant numbers and should not develop an elephant problem. Historically, miombo areas probably supported only relatively low elephant densities. But some miombo areas have now been severely impacted by elephant, probably to a large degree the result of compression leading to unusually high elephant numbers, e.g. in Chizarira NP (Thomson 1975). In many cases it is probably true that elephant impacts have been more severe in woodland on heavier textured soil where infiltration is impeded and soil nutrients fairly high, e.g. mopane woodlands in Hwange NP compared to Kalahari sand woodlands (Cumming 1981a). Two studies of long-term change in vegetation cover using aerial photographs in Kruger NP (Trollope *et al*. 1998; Eckhardt *et al*. 2000) and one in Hwange NP (Rogers & Chidziya 1997) indicated greater declines in woody cover on clay soils than sandy soils, where cover may even have increased. These studies did not specifically link changes to elephant impacts, but they were certainly a factor in combination with fire.

15.3.7 Variation in Annual Rainfall

The effect of low rainfall or an early end to the wet season has the effect of lengthening the dry season, when elephants eat more woody parts and do more damage to trees. This also raises awareness of the problem so that concerns about damage often follow a season of low rainfall (van Wyk & Fairall 1969, Cumming 1981a). At Ruaha, bark stripping was more prevalent in a dry season following a season of low rainfall (Barnes 1982), while Chafota (2000) recorded unusually high damage to the Linyanti riverine vegetation following low rainfall and an early end to the wet season. There were indications that baobab damage at Mana Pools National Park, Zimbabwe may have been greater following low rainfall (Swanepoel 1993), and there was extensive tree damage in Kruger during two successive low rainfall years (Owen-Smith 1988).

15.3.8 Relationship Between Elephant Impact, Fire and Frost

Fire and frost have similar effects on the vegetation in that above ground parts of woody plants are killed, the most affected component of the vegetation usually being the shrubs. Both factors have the effect of removing this food source causing elephants to concentrate their feeding activity on the trees, thus resulting in higher than usual damage to this component (Conybeare 1991). In Chobe, *Burkea africana* appeared to sustain more damage after a fire than in an unburnt area (Chafota 2000). Alternatively, if unburned areas are available after extensive fires, elephant feeding activities may be concentrated there (Bell & Jachmann 1984). If a fire occurs early in the dry season, elephants may even be attracted to the burned area when the plants resprout as was found in Niger, West Africa (McShane 1987). In Kruger NP elephant utilized 32% of mopane shrubs in early burnt plots compared to 57% in control plots, so fire did not completely discourage herbivory, but elephants were not shown to feed preferentially on burnt mopane as had been suggested (Kennedy 2000).

When vegetation has been modified by elephant it may be more susceptible to damage by both fire and frost. Opening up the tree canopy may lead to higher grass fuel loads and fiercer fires that kill regenerating woody plants so that elephants and fire have a synergistic effect (van Wyk & Fairall 1969, Thomson 1975, Guy 1989, Trollope *et al*. 1998). In the case of frost, tree loss causes the reduction in the insulating canopy and allows frost to penetrate the understorey. Coppice regrowth from a broken tree may also be in the height range affected by frost, whereas the undamaged tree would be unaffected (Conybeare 1991).

15.4 IMPACTS ON OTHER ANIMALS

15.4.1 Direct Impacts

Under natural conditions elephants rarely interfere with other species, although conflict may arise in unusual circumstances such as congestion at a water source. White and black rhinos have been killed by elephants under somewhat unnatural circumstances in Pilanesberg National Park and Hluhluwe-Umfolozi Park in South Africa after young male elephants were introduced to areas where there was no established population (Slotow *et al.* 2001, Slotow & van Dyk 2001).

15.4.2 Indirect Impacts

Changes to vegetation structure and floristic composition must have effects on abundance of at least some other species. Such changes may contribute to increased species diversity in circumstances where modification of the vegetation results in the replacement of homogeneous stands of closed woodland or thicket by mosaics of woodland and grassland (Owen-Smith 1987). At Addo Elephant NP in South Africa in succulent coastal thicket, opening up of dense thickets by elephants led to an increase in numbers of browsers such as eland and kudu as more browse became available (Hall-Martin, in Owen-Smith 1987). In Hluhluwe NP the elimination of elephants in the late 1880s was followed by an increase in density of woody vegetation with the subsequent loss of three species of grazing ungulates and reduction in the numbers of others.

In Amboseli, Kenya, outside the area of focus of this review, the most equitable mix of browsers and grazers was found in a mosaic of woodland-grassland with moderate elephant density (Western, 1989). Plant species richness was low in dense *Acacia xanthophlea* woodland and higher where tree density had been reduced by elephants, allowing the entry of other plant species and some grazing animals. Conversely, where elephant density was very high, species richness was reduced. After elephants had caused extensive modification to the vegetation, bushbuck and lesser kudu disappeared (Western & Gichohi, in Cumming *et al*. 1997) and later, giraffe and gerenuk were also lost (Western, in Whyte *et al*., in press). Changes to woodland structure at high elephant density in Tsavo East NP, Kenya were linked to declines in abundance of browsing ungulates and increases in grazers (Parker 1983).

In the Four Corners area, the loss of large areas of riverine woodland in Chobe NP as a result of elephants was thought to have caused a decline in the density of bushbuck (Simpson 1978). Later work showed that compared to a study 20 years earlier, bushbuck were only found in isolated pockets of favourable habitat (Addy 1993). In the best remaining habitat, bushbuck density was 34% of that found previously and in other areas only 2% of former levels.

The effects of reduction in woody biomass and tree height may have more complex effects than merely an increase in the amount of grass leading to increased food availability for grazers. The species composition of the grass sward is likely to change with the reduction in shade and the new species may be of lower quality. An increase in coppice growth may even lead to a reduction in grass biomass. In Kasungu NP it was thought that modification of the miombo habitat had adversely affected sable antelope and Lichtenstein's hartebeest (Bell 1981), while in

Chizarira NP populations of large mammals other than elephant (particularly sable and tsessebe) declined when woodland was severely modified (Cumming 1981b). Large numbers of elephants also trample grass, making it unavailable to grazers (Cumming & Cumming 2003).

Valeix (2002) analysed the annual 24-hour water point game count records in Hwange NP for changes in trends after elephant culling ceased in 1987. As the number of elephants recorded increased, the numbers of impala and kudu, the other most abundant browsers declined. Unexpectedly, the numbers of reedbuck, waterbuck, sable and warthog also declined, but it was not possible to link these declines to the effects of elephants. Although habitat changes and competition for water may have affected these species, it is likely that other factors were also involved.

In the Matetsi area of north-west Zimbabwe elephant numbers were low when the area was used primarily for cattle ranching, and remained low after the land use changed to safari hunting. In 1982, following a year of very low rainfall, many elephants came into the relatively well-watered area and remained permanently, causing a big impact to springs by trampling (V. Booth, pers. comm.). Some of these springs stopped flowing which was thought to have led to the drying of grassy drainage lines downstream and subsequent invasion by woody species, with deleterious effects on selective grazers such as sable.

At elephant-impacted sites in miombo woodland in Zimbabwe, where total tree density had been reduced by 40% and large tree density by 70%, Cumming *et al*. (1997) found that species richness of woodland birds, ants and mantises was significantly lower in impacted woodlands than in relatively intact woodlands, while there was no significant difference in the number of species of other birds or bats. Four of the bird species missing from the impacted woodlands were miombo endemics and several others were species largely confined to miombo woodland. The bat and insect data were later analysed in more detail by Fenton *et al*. (1998). Where the impacted and intact sites were in close proximity (<5 km apart) bat species richness, abundance and activity were significantly greater at intact than impacted sites. In contrast, where the sites were further apart (>20 km) there were no significant differences, and in fact the number of species and total number of bats caught was greater at impacted sites. There were no significant differences in the total number of insects or total numbers of beetles and moths caught in light traps in impacted and intact woodlands. Altogether, the findings did not show that the loss of tree canopy had a significant impact on bats. In another investigation of diversity in impacted and relatively intact woodlands in Chobe NP, there were significantly fewer species and lower abundance of soil animals in impacted riverine woodlands (Dangerfield 1993). In general, soil and litter fauna other than termites and ants were lost when canopies were opened. Termites and possibly ants may benefit from increased woody litter from felled trees.

Bird diversity in habitats impacted by elephants was studied in northern Botswana by Herremans (1995). Comparing numbers and species of birds between highly modified woodland on the Chobe River with less impacted woodland on the Linyanti River some 100 km away, he found seven canopy species present on the Linyanti to be absent from Chobe. Looking at generalist species, there were 249 birds in 18 species on the Chobe compared to 444 birds in 32 species on the Linyanti. Ground and thicket birds were, however, more abundant on the Chobe with 275 birds in 8 species compared to 84 birds in 6 species on the Linyanti. In another study, some gallinaceous birds were also found to respond positively to habitats modified by elephant in Chobe NP (Motsumi *et al.* 2003). Herremans (1995) also sampled mopane woodland in Moremi Game Reserve where there was a mosaic of tall woodland and short coppice shrubland as a result of elephant impact. There were no significant differences in numbers of species in woodland and shrubland but the number of individuals in the canopy and generalist categories was higher in the

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low-impact woodland. In spite of these differences, using a number of different diversity indices, it was concluded that there was no dramatic overall reduction in bird diversity in high-impact sites in either riverine or mopane communities. In the results from the mopane community, the mosaic of high and low impact woodland may not have been the same in a situation where all the tall woodland had been converted to shrubland over a much larger area. Birds that nest in tall trees for example, must move to other areas if all the tall trees are felled; bird species diversity is correlated with foliage height diversity (MacArthur, in Cumming *et al*. 1997). The loss of baobabs at high elephant densities has been discussed earlier. This tree is an important nest site for a number of bird species and hollow baobabs are the only known natural nesting sites of both the Mottled Spinetail (*Telecanthura ussheri*), Bohm's Spinetail (*Neafrapus boehmi*). The Cape Parrot (*Poicephalus robustus suahelicus)* and Mosque Swallow (*Hirundo senegalensis*) also favour baobabs for nesting (Whyte 2001).

15.5 SUMMARY OF MAIN FINDINGS

1. Elephants affect vegetation primarily through their feeding habits. Although catholic in their diet, they do select some species and avoid others. They eat grasses and woody plants but most grazing takes place during the wet season, hence they are thought not to have an important impact on grasses.

2. When browsing, elephants feed mostly between 1 and 2 m above ground, so shrubs are more affected than trees. However, shrubs are more resilient to damage, being able to replace lost biomass more quickly than trees. Elephant feeding results in biomass reduction or death of selected shrubs.

3. Elephants damage trees by pushing them over, breaking the main stem, removing branches and by debarking. Many damaged trees survive as coppice regrowth, but some are killed, either directly or from secondary causes such as woodborers. Tree damage may be greater when available shrub biomass is reduced by factors such as drought or fire.

4. The effect of elephants is to change the physiognomy of woodland, and wooded bushland in particular, by reducing the number of trees. They also change species composition if heavily used species decline in abundance or biomass and avoided species increase. Tree species that have been severely impacted in the review area include *Acacia erioloba, A. nigrescens, A. tortilis, C. mopane, Adansonia digitata, Brachystegia boehmii, Commiphora ugogensis, Combretum collinum, Terminalia sericea, Sclerocarya birrea* and *Faidherbia albida*. Species that have been reported to have increased in abundance following elephant impacts include *Ochna pulchra, Lonchocarpus nelsii* and *Combretum mossambicense*.

5. As a result of tree breakage, there may be an increase in shrub density from coppiced trees, but shrub species composition will be changed and density may also ultimately be reduced. Tree regeneration is slowed or arrested by elephants and other browsers, and also by fire and frost.

6. Because of different species composition and levels of utilisation by elephants, some vegetation types, such as riverine woodland, miombo and mopane woodlands and *Baikiaea* woodland, are more affected than others. Utilisation of particular species may even vary geographically, perhaps affected by soil type and the array of other species available.

7. Impacts of elephants on vegetation are positively related to elephant density, but the rate and amount of vegetation change is affected by a number of factors, such as proximity to water,

variation in annual rainfall, fire, frost and soil type. Changes to vegetation brought about by elephants result in greater susceptibility to the damaging effects of fire and frost.

8. At low to moderate densities the impact of elephants may increase habitat heterogeneity, particularly in a homogeneous environment. This may in turn lead to an increase in biodiversity. At high densities, the opposite probably occurs.

9. Even at low overall elephant density there will be areas of relatively high elephant concentration where impacts will be more severe. This non-uniform spatial distribution makes it difficult to quantify the relationship between elephant density and impacts on vegetation. Miombo woodland may be destroyed at elephant densities of 0.2-0.5 elephants per km^2. Even at an elephant density of 0.13 per km^2 there were areas of severe vegetation damage in the Kruger National Park.

10. Vegetation change caused by elephants affects other species of animals; arboreal birds are particularly vulnerable and there is evidence that gross vegetation change will also result in declines in numbers of most other browsers and possibly some grazers. Very high elephant numbers may also affect other species through competition for water.

11. Changes to woodland structure affect the herbaceous layer, but these changes and the effect of vegetation change on grazing animals have not been fully investigated.

12. When elephants recolonise an area from which they have been absent for some time, impacts are likely to be dramatic.

15.6 DISCUSSION OF FINDINGS

All over southern Africa the proclamation of Game Reserves with protection from hunting and the elimination of competition from people, has allowed elephant numbers to increase. In these areas, as elephant density has increased, vegetation change resulting in declines in tree density has been apparent. It is, however, uncertain whether the well-developed woodlands found in the early part of this century had been in place for a long time or were a relatively recent phenomenon that had developed after elephant numbers were reduced to unusually low levels by ivory hunting. In this hypothesised scenario, present elephant densities and the state of woodlands are similar to what may have pertained before excessive hunting reduced elephant populations. In some areas, notably Hwange National Park, the provision of artificial water supplies where surface water was seasonal has also contributed to the increase in numbers.

Although elephants feed primarily on shrubs and small trees, their impact on large trees is more conspicuous as shrubs are able to replace lost biomass more quickly. This loss of canopy trees has been particularly noticeable in riverine woodlands, for example in Chobe and Sengwa (Child 1968, Anderson & Walker 1974). Riverine woodlands usually comprise a very small proportion of any particular area, but other more widespread vegetation types such as miombo and mopane woodlands, have also been dramatically altered (Guy 1981). Common species that have been heavily impacted upon in different areas include *Acacia nigrescens, A. erioloba, A. tortilis, Adansonia digitata, Sclerocarya birrea, Terminalia sericea, Colophospermum mopane* and some *Combretum* species. In spite of their greater resilience to damage, shrub abundance may be altered and particular species may be virtually eliminated from certain vegetation types, such as *Grewia flavescens* in riverine woodland at Sengwa and aloes in Kruger NP. Much impact on small shrubs and seedlings is probably overlooked as these can be pulled out of the ground leaving nothing behind.

As highly impacted upon species have declined, less impacted upon species have increased in importance and in density, changing the floristic composition of the vegetation in addition to the structure, for example in miombo woodland at Sengwa (Mapaure 2001), riverine woodland in Chobe (Addy 1993) and bushland in Hwange (Conybeare 1991 and unpublished data). Some trees coppice readily when their stems are broken, for example *C. mopane*, and can be maintained as shrubs by regular browsing (Caughley 1976). It has been argued that these coppice trees supply more browse at an available height for elephant and other herbivores (Smallie & O'Connor 2000, Styles & Skinner 2000), but in times of stress such as a drought, they are more likely to die than undamaged trees (Lewis 1991, Conybeare 1991).

If the density of coppiced trees is high, grass growth may be suppressed to the disadvantage of grazing animals (Bell 1981). But more commonly canopy thinning by removal of large trees leads to a higher grass biomass. This has two implications: (a) higher fuel loads resulting in more frequent, hotter fires, and (b) probable change in grass species composition with an increase in taller, coarser grasses. Such grass species may favour the coarse grazers, but they disadvantage selective grazers adapted to woodland situations, for example sable antelope and Lichtenstein's hartebeest. Where fires are frequent, fire and elephants can have a synergistic effect where the destruction of large trees leads to hotter fires which, together with browsing by elephant and other species, can stop or slow further tree recruitment. In places where severe frost occurs, woodland damaged by elephant may be more susceptible to frost damage. Fire and frost, by killing vegetation at lower levels where elephants obtain most of their food, may result in greater elephant attention to taller trees where the foliage is unaffected (Chafota 2000).

If dominant trees are not eaten, damage may be less noticeable. But changes will still occur if associated species are heavily impacted upon and decline, for example in *Baikiaea* woodland on Kalahari sands. In *Baikiaea* woodland, where elephant pressure was high in Chobe, there has been an apparent decline in the area of woodland (Mosugelo *et al.* in press).

While elephant density is clearly the most important factor governing the impacts of elephant on vegetation, the size of the elephant range, the patterns of elephant distribution, the distribution of permanent surface water, floristic and physiognomic composition of the vegetation and elephant occupancy of different habitats will all influence the pattern and scale of impact. The effects of elephants are not uniform across its range. This means that even at low densities, there will be areas of relatively high occupancy and effectively higher density that will show greater impacts. Water sources are particularly important foci of elephant concentration and vegetation change. In Hwange, Conybeare (1991) showed that even at an overall density of 0.4 elephants per km^2 the effective dry season density within 1 km of permanent water points could be 2.7 per km^2, at which level impacts would be high. In fact, elephant densities over most of the elephant range of south-central Africa are much higher, and dry season densities in close proximity to water points commonly reach 7-10 elephants per km^2. Even around seasonal water points density may be as high as this while water is available (Ben Shahar 1993). Locally severe impact to the vegetation at such sites is inevitable, even if overall density is relatively low.

In most cases the changes resulting from high elephant numbers are probably reversible. There are some examples where there has been a reversal of the trend in vegetation following a reduction in elephant density, for example in riverine *Acacia* woodland at Sengwa (Coulson 1997). However, changes may not always be reversible as an increase of or invasion by non-palatable or fire-resistant species may alter the composition for a long time, if not permanently, for example in miombo woodland at Sengwa (Mapaure 2001). In some circumstances vegetation may remain in a "fire trap" (Bell 1984) where fire alone, without elephants, maintains a changed state.

Direct impacts of elephants on other animal species are rare, but indirect effects through habitat modification may be more widespread. A reduction of woody biomass by elephants has been shown to adversely affect some browsers in East Africa, although there is less documented evidence from south-central Africa. However, the loss of riverine woodland at Chobe seriously affected bushbuck (Addy 1993) and possibly kudu (Simpson 1975). Any large-scale change in physiognomy and floristic composition of the vegetation will undoubtedly have an effect on other browsers. Modification of habitats leading to changes in the herbaceous layer may be beneficial to some coarse grazers and adversely affect other grazing herbivores such as sable and tsessebe, but there has been no real proof of this. Although changes in the vegetation in Hwange NP resulted in lower plant species diversity, and there are recorded differences in species composition of birds and some invertebrates between impacted and intact woodlands (Cumming *et al.* 1997, Herremans 1995), no clear evidence of loss of biodiversity has yet been demonstrated.

15.7 FUTURE TRENDS AND IMPLICATIONS FOR THE FOUR CORNERS CONSERVATION AREA

As elephant numbers increase in south-central Africa, and in the absence of any population reduction by culling or poaching, there will be a decrease in the area of woodlands and an increase in the extent of shrubland and wooded and bushed grassland. The development of large areas of grassland, as happened in East Africa (Laws 1970), seems unlikely because of differences in climate and soils. Grassland development will probably be confined to smaller areas such as the immediate vicinity of water points. The rate of vegetation change in different localities will depend on its species composition in addition to elephant density. Associated with these physiognomic changes will be changes in abundance of many plant and animal species. Such changes in abundance will not necessarily happen quickly and long-term monitoring will be needed in order to detect it. Apart from vegetation changes, in areas where dry season surface water is limited any competition for the scarce resource will adversely affect other smaller, water-dependent animals. Large numbers of elephants will cause seasonal pans to dry more quickly, which will in turn affect other mobile water dependent animals forcing them back to the vicinity of permanent water sources.

In the Four Corners area it must be assumed that elephant numbers will continue to increase but the proportional increase in density will be alleviated slightly by range extension to the west and north. The riverine habitat of the Chobe River may have stabilised, while on the Linyanti River it will continue to change by a general opening of the canopy woodland with reduced abundance of some tree and shrub species and an increase in others. Tree density in *Acacia* woodlands that are not strictly riverine, for example at Savuti, will also continue to decline. In the Kalahari sand woodlands tree cover will continue to decline under the influence of elephant browsing, fire and frost; a slow decline in the density of large trees is probable. These changes will be greatest close to permanent and seasonal water points but will probably be slower than in other vegetation types. Areas dominated by mopane may stabilise with a higher proportion of coppice although much of the coppice will probably be eventually eliminated. Again the rate and extent of change will be influenced by proximity to surface water, particularly permanent water. Plant communities dominated by mopane surround many of the seasonal pans and these are likely to be heavily impacted upon.

The final outcome may be an equilibrium where elephants are limited by resources available within range of late dry season water supplies. By that time the vegetation in those concentration areas will be considerably changed and adverse conditions such as drought will probably cause significant mortality among elephants, as has been recorded previously on the border between Hwange NP and Botswana (Conybeare & Haynes 1984). Any climatic change that results in greater extremes of rainfall is likely to accelerate the process. A breakdown in the artificial supply of water in Hwange could also trigger higher mortality of elephants and other species. If water remained in short supply there, elephants might possibly move to other areas such as Chobe NP.

In response to changes in the structure and composition of the vegetation, there will probably be a decline in abundance of some browsing animals, selective grazers and arboreal birds. At the same time there may be an increase in abundance of other grazers and mixed feeders such as impala if available habitats become more suitable for them. There is already evidence that impala may be responding positively to habitat changes in Chobe NP (Rutina *et al.* 2003).

15.8 FUTURE RESEARCH REQUIREMENTS

There are many papers addressing the impact of elephants on vegetation but surprisingly few long-term monitoring projects that show what changes take place in terms of changing species composition and dominance. One reason for this paucity is probably that such projects are not suitable for post-graduate degree studies. These problems need to be addressed in other ways. Most long-term studies that have been done are retrospective analyses of aerial photographs, but there are no field data associated with the earliest photographs so that any analysis of perceived changes in terms of species composition is difficult. Focusing on a single important species also tells only part of the story. It is not sufficient to know that there has been a decline in a particular species; it is as important to know the implications of that decline. Does another species replace the declining one and what are the effects of the change for other animals and plants?

The major gaps in knowledge on the effects of elephant impacts on vegetation are the indirect effects of habitat modification on other species and biodiversity in general. These have important implications for conservation of biodiversity in protected areas, particularly where such areas are already islands in highly modified surroundings. They are the type of issue that should be addressed in future research. The current BONIC project in Chobe NP may be doing this in one area.

Priority research projects include:

a) long-term vegetation monitoring, perhaps using repeatable air photo transects or plots linked to permanent ground sites in order to monitor the full range of change taking place to the vegetation;

b) monitoring the numbers of a representative range of other ungulates, particularly those not easily counted from the air, and also taxa other than mammals.

Wherever possible these monitoring projects should have control sites where elephants are either absent or in low numbers. Another approach would be a comparison of the fauna in impacted and intact habitats along the lines used by Cumming *et al.* (1997), but on a more extensive scale. Great care would be required to ensure that the sites were in fact comparable and that elephant impact was the only factor differentiating the sites.

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