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Review

A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa

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ABSTRACT

An hypothesis predicting which woody species selected by elephant are at risk of local extirpation is based on an understanding of elephant digestive physiology, foraging ecology, attributes of individual plants and populations, and historical changes in ecosystems. Elephant select items rich in cell solubles relative to availability for achieving maximum throughput per unit time on account of their large energy requirement, hindgut fermentation with limited cell wall digestion, high passage rate, and inefficient recycling of microbial protein. Accordingly, diet is predominantly green grass and herbs in the wet season, green browse in the late wet and dry seasons, and bark and roots following leaf fall. Increased consumption of woody material indicates nutritional stress. Bulls graze more than cows and impact woody plants more when grazing deteriorates.

Species vulnerable to extirpation by elephant are those: whose attributes predispose adults to pollarding, uprooting or ringbarking; adults coppice poorly, hence mortality occurs; mortality is not compensated by regeneration and recruitment owing to the impact of elephant and other agents; species have a restricted distribution; and poor dispersal ability constrains recolonisation. Threat of their local extirpation has increased because of an increased probability of encounter with elephant attributed to artificial boundaries that have constrained movement, and proliferation of water points that has reduced spatial refuges for plants and weakened density-dependent regulation of elephant populations. Degradation of grasslands, wetlands and riparian areas has forced elephant to subsist on woody vegetation for a longer period of the annual cycle. A reduction in water points should increase local elephant density and attendant density-dependent effects of increased foraging distance, nutritional stress, calf and juvenile mortality, and predation, and reduce reproduction. Eliminating human predation after 4000 years in some parks has contributed to the problem. Mitigation of the threat of local extirpation should concentrate on configuration of boundaries, water provision, simulated predation, minimum reserve size, and not pursue non-definable notions of elephant carrying capacity.

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1. Introduction

Elephant can have a dramatic impact on their habitat. The 'elephant problem' emerged in the 1960s on account of elephant-mediated transformation of forest and woodland to open savanna or grassland throughout Africa (summaries: Eltringham, 1982; Owen-Smith, 1988; Spinage, 1994). These dramatic changes in vegetation were brought about by elephants, often in combination with other factors such as fire, incurring elevated mortality of mature trees and suppressing recruitment and regeneration. The problem was precipitated by compression of elephant populations into parks in response to expanding human settlement (Laws, 1970b; Cumming, 1981a, 1982; Barnes, 1983b; Lewis, 1986; Hanks, 1979). Concern prompted authorities to initiate culling of elephants in a number of reserves in an attempt to halt woodland loss. Thereafter poaching decimated elephant populations in east Africa in the 1970s and 1980s (Eltringham and Malpas, 1980; Douglas-Hamilton, 1987; Barnes and Kapela, 1991), which curtailed woodland loss (Barnes et al., 1994; Leuthold, 1996), but high elephant densities and associated woodland loss have persisted in southern Africa (Conybeare, 2004). The validity of concerns about increases in elephant populations, resistance to culling, challenges that elephant 'damage' has been ill-defined, and debate about the manner of savanna functioning (Gillson and Lindsay, 2003), demand a greater understanding of the impact of elephant on vegetation.

Impact of elephants on woody vegetation has lead to concern about possible extirpation of plant species and of animal species whose persistence is dependent on forest or woodland habitat (Cumming et al., 1997; Fenton et al., 1998; Lombard et al., 2001; Botes et al., 2006). The consequence of elephant impact on woody species varies markedly from local extirpation (Laws et al., 1975; Moolman and Cowling, 1994) to persistence in the face of continued utilisation (Lewis, 1991; Styles and Skinner, 2000). No clear prediction has emerged about which woody species are prone to extirpation and under what circumstances.

Further concern about elephant impact on biodiversity has emerged in southern Africa over the past two decades. Elephant populations have been re-established in a number of small- to medium-sized reserves (<1000 km²) in order to (a) serve the tourism industry, which involves conversion of live-stock ranches to wildlife reserves, (b) expand the meta-population, and (c) maintain key ecological processes through their role as a keystone species (Western, 1989). Biodiversity conservation is now a key mandate for most reserves. This paper catalogues such reserves with low elephant densities by comparison with some national parks, yet extirpation of certain woody species is considered imminent although widespread conversion of woodland may not have occurred. Elephant and these threatened species have previously co-existed at some spatial scale, begging the question of what ecosystem changes have occurred to disrupt this relationship?

Management intervention has been constrained by lack of a predictive ability about elephant-woodland relationships for ensuring their co-existence with selected food species. Research has progressed from the necessary descriptive studies of elephant population numbers and trends, diet, and impact on vegetation (summarised in Eltringham, 1982; Owen-Smith, 1988; Spinage, 1994), to study of plant-herbivore dynamics (Laws et al., 1975; Caughley, 1976; Barnes, 1983a; Pellew, 1983; Dublin et al., 1990). Such study generally focussed on dominant species rather than on plant diversity, but it has revealed that sexes differ in their impact on woody vegetation (Guy, 1976) as a consequence of the expected influence of a twofold difference in body size on ecology (Owen-Smith, 1988), and should therefore be considered separately.

The aim of this paper is to develop an hypothesis of the relationship between elephants and vegetation that can predict which species are vulnerable to local extirpation and under what circumstances, and explain differences and consistencies in patterns of elephant impact across a range of African reserves and ecosystems. The hypothesis is founded upon a functional approach to the elephant-vegetation relationship, and is comprised of three main components. (1) The influence

of body size, sex and digestive physiology on foraging ecology in relation to seasonal variation in food supply is used as a basis for predicting the selection and utilisation of vegetation types and species by elephant. (2) The attributes of an individual plant or plant population which render a plant species vulnerable to local extirpation by elephant impact are predicted. (3) The characteristics of a reserve or ecosystem that would predispose a woody species to extirpation by elephant are identified.

2. Elephant foraging ecology (developed by BC)

2.1. Elephant digestion

Body size and the nature of the digestive system of elephant are used to provide a theoretical framework for predicting their pattern of forage selection (following Hanley, 1982); empirical evidence follows. Food requirement of an animal increases with increasing body weight as a result of increasing costs of maintenance and growth (Owen-Smith, 1988). The absolute daily nutrient requirement of elephant is therefore larger than that of any other terrestrial mammal, and that of a bull elephant greater than that of a cow. Consequently, elephant need to ingest more nutrients per unit foraging time than smaller mammals, and bulls more than cows or calves. Elephant should therefore favour food types that permit a rapid rate of nutrient intake, which should be more pronounced for bulls than for cows or calves.

From a herbivore foraging perspective, plant cells can be divided into cell solubles contained in the cytoplasm and cell wall material encasing the cytoplasm. Cell solubles, which include proteins, sugars, starch and lipids, are digested rapidly and almost completely. By comparison, cell wall fibre, which includes hemicellulose, cellulose and (mostly indigestible) lignin, is slowly digested. Elephants are hindgut fermenters (Van Hoven et al., 1981). Unlike ruminants, their digestive system does not have blocking structures that limit the rate of passage of material through the gut. Their retention time of ingesta is as short as 14 h compared to 70–100 h in ruminants, even for coarse material (Eltringham, 1982; Owen-Smith, 1988). Short passage time results in fermentation of slowly digested cell wall material, in particular cellulose, being limited, not owing to inefficient digestion per unit time but to the limited time spent digesting (Van Hoven et al., 1981; Meissner et al., 1990). As a consequence of cell wall material not serving as an important energy source, elephant should be more reliant on easily digested cell solubles than herbivores whose main energy source is derived from digesting cellulose more completely. Dependence on cell solubles is heightened by their inefficient recycling of microbial protein compared with ruminants because of their hindgut digestive system in which most microflora are lost in faeces (Janis, 1976; Hanley, 1982). The importance of cell solubles combined with the poor rate of digestion of cell wall material increases the importance of chewing for rupture of cell walls and release of cell contents. Bulls exhibit slower ingesta passage rates than cows (Clauss et al., 2003) and therefore can utilise food with high fibre content (e.g. grass) more than cows (Buss, 1961; Guy, 1976). Rate of ingestion

should therefore be more important for foraging decisions by bulls than by cows.

In summary, a rapid passage rate allows elephant to meet their high absolute nutritional demands by maximising intake of foods rich in easily digestible cell solubles in order to compensate for their short gut passage time, limited digestion of cell wall, and inefficient recycling of microbial protein.

2.2. Nature of preferred food types

The preceding section predicts that elephant optimise their diet by selecting food types offering the highest intake rate of cell solubles, commonly indexed by digestible protein (Owen-Smith, 1988). Intake rate is determined by protein concentration and ingestion rate, which can compensate for one another. Protein concentration of browse can be up to twice that of grass during the growing season and is more constant over the annual cycle (Dougall et al., 1964; Field, 1971; Field and Ross, 1976; Topps, 1997). Protein concentration of green grass is high during the growing season when a high intake rate can be achieved on account of herbage density, but protein concentration declines markedly as the dry season progresses (Field, 1971; Osborn, 2004). Intake of senescent or structural material should be avoided because of its lack of cell contents.

Short-term intake rate of digestible protein is influenced by time to gather a trunk load, mass of a trunk load, handling time (chew and swallow) per mouthful, and protein concentration (distance and speed of travel between food patches is assumed constant) (Spalinger and Hobbs, 1992; Farnsworth and Illius, 1996, 1998). Elephant should prefer those foods from which the greatest amount of digestible protein can be sequestered per unit time. During the growing season, browse usually has a higher protein concentration than grass and handling times are similar, but a greater mass intake rate, hence total digestible protein, is realised from grass because larger trunkloads can be ingested than of woody foliage (Clegg, unpublished data). Elephant select for soft, broad-leaved grasses (e.g. *Panicum*, *Urochloa*) and soft-bodied herbs with a high ratio of cell contents to structural material, whose cell contents are relatively easily released with chewing, not necessarily grasses selected by ruminants (Field, 1971; Williamson, 1975b). Ingestion rates of bark or woody roots are the slowest because of the time taken to harvest and chew. Food items can therefore be arrayed in terms of the potential intake rate of cell solubles, from green grass swards offering the highest to woody roots the lowest.

Bulls should utilise more grass longer into the dry season than cows because their larger body size, hence larger mouthfuls (Stokke and du Toit, 2000) allows a greater rate of mass intake that compensates for a lower density of cell solubles. This prediction is consistent with the large proportion of a bull's diet constituted by green grass when it is available (Buss, 1961; Guy, 1976), whereas cows concentrate on woody browse (Barnes, 1982).

2.3. Seasonal variation in diet

The diet of elephant shows a strong seasonal pattern in markedly seasonal environments that is consistent with the

theoretical predictions presented above. Elephants characteristically select green grass and herbs during the rainy season when all food types are abundant, browse is eaten throughout the year but intake of browse foliage increases with the onset of the dry season when little green grass is available, and consumption of bark and tree roots increases toward the end of the dry season once browse foliage begins to fall (Buss, 1961; Napier Bax and Sheldrick, 1963; Laws, 1970a; Field, 1971; Poché, 1974; Wyatt and Eltringham, 1974; Laws et al., 1975; Williamson, 1975b; Guy, 1976; Field and Ross, 1976; Barnes, 1982; Owen-Smith, 1988; Viljoen, 1989; Ruggiero, 1992; Kabigumila, 1993; Tchamba and Seme, 1993; De Boer et al., 2000; Osborn, 2004). Elephant will continue to feed on green grass well into the dry season in those habitats (e.g. swamps) in which it is abundantly available (Buss, 1961; Buss and Savidge, 1966; Croze, 1974a; Wyatt and Eltringham, 1974; Eltringham, 1977; Western and Lindsay, 1984; Lewis, 1986; Tchamba and Mahamat, 1992; Kalempera, 1989; Kabigumila, 1993). High quality items like fleshy fruits and pods are highly sought after but rarely available in substantial quantities (Buss, 1961; Williamson, 1975b; Field and Ross, 1976; Lewis, 1986; Viljoen, 1989; Tchamba and Seme, 1993). This seasonal variation in diet is consistent with elephant ensuring a near maximum intake rate of material with a large absolute amount of extractable cell contents relative to what is available. Bark is judged to be consumed mainly for its sugar-containing phloem tissue, as it is most consistently utilised during early spring when sap flow through phloem is most active for flowering or leaf flush (Croze, 1974b; Williamson, 1975b; Field and Ross, 1976; Barnes, 1982; Childes and Walker, 1987; Owen-Smith, 1988; Swanepoel, 1993) and concentration of secondary chemicals lowest (Styles and Skinner, 2000), and relations between bark consumption and other nutrients have been inconsistent (none shown in Anderson and Walker, 1974 or Thomson, 1975; greater nitrogen concentration of cambial tissue in preferred species shown by Hiscocks, 1999).

The influence of body size and digestive physiology on foraging ecology thus have the potential to affect the success of woody species. Elephant diet during summer, in particular of bulls, should be composed mainly of green grass when it is available. Their impact on woody plants should therefore be lower during years with extended wet seasons or years with above-average rainfall because green grass will be more available. When green grass is less available during drought years, elephant (especially bulls) are forced to increase consumption of woody leaves, bark and roots earlier in the season when they are relatively the most palatable (Styles and Skinner, 1997, 2000), with a resultant increased impact on woody plants (Napier Bax and Sheldrick, 1963; Williamson, 1975b; Barnes, 1982; Lewis, 1991; Swanepoel, 1993; Osborn, 2004; Birkett and Stevens-Wood, 2005). Owing to greater body size, bulls are primarily responsible for pollarding, uprooting and ringbarking (Guy, 1976; Barnes, 1982; Barnes et al., 1994; Hiscocks, 1999).

An elephant's size and digestive system result in a hierarchy of selection for plant types, species, and plant parts in response to seasonal changes in order to maintain a sufficient rate of intake of food of adequate quantity and acceptable quality. Populations in which the expected seasonal pattern shows an increasing proportion of bark and roots being con-

sumed during the early dry or even wet seasons are likely to be experiencing nutritional stress. Stressed, large bulls in particular will exercise greater damage on woody vegetation (Guy, 1976; Barnes et al., 1994). The age and sex ratio of elephant populations can vary substantially over time (Ross et al., 1976; Aleper and Moe, 2006), with substantial declines in the ratio of males to females as a result of poaching (Lewis, 1984). The consequences of such changes on the impact on woody vegetation have yet to be described, but such an impact has become increasingly apparent in southern African reserves in which a re-introduced cohort of young animals has matured simultaneously (Smallie and O'Connor, 2000).

3. Plant species: key determinants of vulnerability to extirpation by elephant utilisation

Persistence of a plant species within a reserve depends on whether the rate of recruitment and regeneration can match the rate of adult mortality over time. The question is whether elephant utilisation, alone or in combination with other agents such as fire, drought, and other herbivores can force a plant species toward local extirpation through elevating adult mortality or decreasing recruitment or regeneration to unsustainable levels. A list of species that may be heading for local extirpation as a result of elephant utilisation was compiled (Table 1). Its short length is considered to reflect the lack of attention this issue has received. Attention has focused mainly on dominant species and a few icons such as baobabs. Although some woodland in larger reserves may have been lost, their dominant species may persist in coppice form or regenerate easily (Lock, 1977; Pellew, 1983; Starfield et al., 1993). For reserves in which plant diversity has long been a key concern (e.g. Addo NP), there is strong evidence that elephant have caused the extirpation of some species. Similar evidence is emerging for a number of smaller reserves in southern Africa (e.g. in Table 1: Ithala GR; Songimvelo GR; Tuli GR).

Predicting which species are vulnerable to extirpation requires consideration of the following:

- (i) Is the primary impact of elephant on population dynamics of plant species through elevating adult mortality, reducing recruitment from shrubs/saplings, or reducing seedling regeneration?
- (ii) What attributes of an individual plant might affect its selection and manner of utilisation by elephant, which in turn might render it vulnerable to mortality or, conversely, provide tolerance of utilisation?
- (iii) Is elephant impact on mortality, recruitment or regeneration dependent on a synergy between elephant utilisation and other environmental or biotic factors?
- (iv) What attributes of the population biology or ecology of a species might predispose it to local extirpation?

Elephant can incur mortality of adult woody plants or shrubs through complete stem breakage (pollarding), ringbarking, uprooting, or repeated, severe defoliation of foliage, with pollarding and ringbarking being the most common (Table 2). Recruitment of adults from shrubs has been impacted in a similar manner (Leuthold, 1977; Dublin et al., 1990;

Table 1 – Plant species which have been extirpated, or are tending toward extirpation, across a range of African reserves

Reserve	Species	Description of reserve	Elephant population	Impact on plant species	Source
Tsavo East NP, Kenya	<i>Adansonia digitata</i> , <i>Boswellia hildebrandtii</i>	MAR <500 mm; 13,000 km ² ; flat basin with hills, few perennial rivers	1.2 elephant km ⁻² in late 1960s; 15% died in drought of 1970–1971; subsequent poaching reduced population to low density	Baobab killed at 2% per annum in 1967, effectively extirpated by 1974; recovery post elephant collapse unknown. <i>B. hildebrandtii</i> , a species restricted to thicket, disappeared from monitored plots	Laws (1970b), Leuthold (1977), Van Wijngaarden (1985)
	<i>Commiphora</i> spp.			Dominant: 95% of adults and shrubs lost by 1976 (90–5 ha ⁻¹) between 1970 and 1974; substantial regeneration potential; recovery by 1994 following collapse of elephant population	Leuthold (1977, 1996)
Lake Manyara NP, Tanzania	<i>Adansonia digitata</i>	MAR 750 mm; 90 km ² ; lake basin with surrounding flatlands rising steeply to escarpment	4.9 elephant km ⁻²	Minimal damage in 1969, 1% mortality per year by 1981; absolute refuges on escarpment preclude extirpation although slopes may be cleared	Weyerhauser (1985)
Msembe, Ruaha NP, Tanzania	<i>Adansonia digitata</i>	MAR 580 mm; 130 km ² ; <i>Commiphora</i> – <i>Combretum</i> woodland; ridge between rivers	2.41 elephant km ⁻² in 1977; population approximately halved by poaching in 1980s; density in study area maintained but with few bulls	Baobab density of 51 km ⁻² declined by 46% between 1976 and 1982, but remained stable thereafter as elephant bulls were poached	Barnes (1985), Barnes et al. (1994)
	<i>Commiphora ugogensis</i>			Dominant species which declined from ~30 ha ⁻¹ in 1971 to 15 ha ⁻¹ in 1977 to 1–2 ha ⁻¹ in 1982; no regeneration; adults predicted to disappear but coppices; decline of trees arrested by poaching	Barnes (1983a, 1985)
Murchison Falls NP, Uganda	Rabongo Forest: many species	MAR 1000–1250 mm; 3900 km ² ; river headwaters in hill area		Small relict forest: trees ringbarked, grasses penetrated, fire killed resprouts	Buechner and Dawkins (1961)
Queen Elizabeth NP, Uganda	<i>Rhus natalensis</i> <i>Bridelia scleroneuroides</i>	MAR 600–1200 mm; 1979 km ² ; gentle topography; perennial water abundant	Density up to 1.5 km ⁻² in wet season	100% and 77% ringbarking respectively; predicted likely to disappear but regeneration unknown	Field (1971)
Kalamaloue NP, Cameroon	<i>Combretum aculeatum</i>	MAR 500–700 mm; 45 km ² ; flat topography plus floodplain	Floodplain was key dry season habitat for elephant population in north Cameroon; impact on savannas increased post-1986 following desiccation of floodplain by agricultural development	Was a dominant: by 1991 60% killed, 40% damaged; regeneration also selected; suggested as threatened because of loss of floodplain habitat for elephant in winter	Tchamba and Mahamat (1992)
Nazinga GR, Burkina Faso	Shrubs: <i>Annona senegalensis</i> , <i>Combretum nigricans</i> , <i>Cassia sieberiana</i> ; tree: <i>Acacia dudgeoni</i>	MAR 880 mm; 940 km ² ; flat topography (300 m asl)	Former dry season range of 5000 km ² system now used permanently because water supplied; densities up to 2.5 km ⁻²	Near disappearance between 1986 and 1988 resulting from elephant and fire impact; regenerative potential not assessed	Jachmann and Croes (1991)
Chizarira NP, Zimbabwe	<i>Brachystegia boehmii</i>	1910 km ² ; MAR 640 mm; <i>B. boehmii</i> woodland occupies 10% of reserve on watershed	~1.0 km ⁻² in dry season of 1973, up to 1.5 km ⁻² by 1980	Adult trees eliminated from patches by 1973; <i>B. boehmii</i> woodlands lost by 1981; converted to open <i>Combretum</i> woodland; coppice shrubs have persisted but heavily impacted by fire	Thomson (1975), Cumming (1981b, 1982), Starfield et al. (1993)

(continued on next page)

Table 1 – continued

Reserve	Species	Description of reserve	Elephant population	Impact on plant species	Source
Senga Wildlife Research Area, Zimbabwe	<i>Acacia robusta</i> , <i>Brachystegia boehmii</i> , <i>Grewia flavescens</i>	MAR 640 mm; 373 km ² ; dissected topography; southern boundary of Chizirira NP	<1.5 km ⁻² until late 1970s, then increased to 2.9 km ⁻²	<i>Acacia robusta</i> (tree) and <i>G. flavescens</i> (shrub) almost eliminated by 1973, not reported on afterwards; <i>B. boehmii</i> almost eliminated by 1998. Trees killed mainly by ringbarking, resprouts killed by fire; shrub killed by uprooting	Anderson and Walker (1974), Conybeare (2004)
Tuli GR, Botswana	<i>Commiphora merkerii</i> , <i>C. mollis</i> , <i>C. glandulosa</i> , <i>C. tenuipetiolata</i> , <i>Lannea schweinfurthii</i> , <i>Sclerocarrya birrea</i>	MAR 370 mm; ~400 km ² ; mostly gentle topography	Density in 1991 was 0.63 km ⁻² ; gradual compression and population increase over past 100 years	Species were relatively common; species are not effective resprouters; no regeneration; true local extirpation	Page, personal communication, University of KwaZulu-Natal, Durban, South Africa
Venetia-Limpopo NR, South Africa	<i>Adenia spinosa</i>	MAR 370 mm; 350 km ² ; species occurs in hilly terrain but no inaccessible refuge	48 elephant introduced in 1991 (0.14 km ⁻²)	Long-lived succulent; Limpopo valley endemic; no regeneration; 73% mortality by 2002 of an estimated population of 103 attributed to elephant	O'Connor, unpublished data
	<i>Aloe littoralis</i>	Occurs on rocky and flat terrain		Uncommon prior to elephant re-introduction in 1991; none observed during 2002 vegetation survey	
Kruger National Park, South Africa	<i>Aloe marlothii</i>	MAR ~500 mm; small portion of 20,000 km ² . Occurs on steeper topography	Park established in 1905; elephant maintained at ~0.4 km ⁻² until 1994; at 0.7 km ⁻² in 2005	This arborescent succulent lost before 1960; other browsing species (eland, kudu, black rhinoceros) also implicated	Whyte et al. (2003)
	<i>Sclerocarrya birrea</i>			Lost from one habitat, similar trend in others	Jacobs and Biggs (2002a,b)
Addo Elephant NP, South Africa	<i>Aloe africana</i> , <i>Euphorbia mauritanica</i> , <i>Rhigozum obovatum</i> , 7 species of endemic geophytes and succulents	MAR 436 mm; 120 km ² for elephant in 2005; gentle topography; endemic succulent thicket (conservation priority)	Park established in 1931 for 11 elephant; 2.2 elephant km ⁻² in 2005	<i>A. africana</i> lost; 80% loss of <i>E. mauritanica</i> and <i>R. obovatum</i> ; geophytes and succulents: 19 species in elephant exclosures, 12 species in park	Barrat and Hall-Martin (1991), Moolman and Cowling (1994), Lombard et al. (2001)
Ithala GR, South Africa	<i>Acacia davyi</i> , <i>Aloe marlothii</i> , <i>Cussonia natalensis</i> ; <i>Cussonia spicata</i>	MAR 790 mm; 297 km ² ; rugged (350–1550 m asl)	Re-introduced in 1990; Reserve density was 0.19 km ⁻² in 2000 but <half of reserve utilised	All on verge of extirpation from combined impact of elephant, giraffe, black rhinoceros, and other browsers	Bond and Lofell (2001), Wiseman et al. (2004)
Songimvelo GR, South Africa	<i>Aloe marlothii</i> , <i>Cussonia spicata</i> , <i>Pterocarpus angolensis</i>	MAR 800–1400 mm (irt topogaphy); 310 km ² ; rugged (600–1800 m asl); harbours significant plant diversity	Re-introduced from 1992, 36 by 1999; much of reserve not accessible, hence concentrated impact	Low levels of recruitment and high mortality, utilisation not considered sustainable	Steyn and Stalmans (2001)
Welgevonden GR, South Africa	<i>Aloe marlothii</i> , <i>Elephantorrhiza burkei</i> , <i>Pappea capensis</i>	MAR ~650 mm; 300 km ² ; rugged on coarse, infertile sandstones	Small population re-introduced in the 1990s	Severely impacted and likely to become extinct	A. Parker (unpublished) cited in Botha et al. (2002)
Hluhluwe-Imfolozi GR, South Africa	<i>Cussonia spicata</i>	MAR 600–1000 mm; ~1000 km ² ; rolling hills covered mainly by savanna, some grassland and forest	Re-introduced population of about 390 (0.4 km ⁻²) in 2006	Severely impacted by elephant and other browsers	S. van Rensburg, personal communication, ecologist, HIP

Table 2 – Level of elephant-related mortality for selected woody species illustrating the main manner in which mortality is inflicted

Species	Reserve	Mortality (%)	Manner of mortality	Comment	Source
<i>Acacia drepanolobium</i>	Sweetwaters GR, Kenya	1.9 pa	Not described	Rate between 1998 and 2001. Reserve is 92 km ² ; elephant at 1.2 km ⁻²	Birkett and Stevens-Wood (2005)
<i>Acacia erioloba</i>	Namib desert, Namibia	1.6	Ringbarking	Accumulated mortality up until time of survey	Viljoen and Bothma (1990)
<i>Acacia gerrardii</i>	Kidepo NP, Uganda	10.8 pa	29% ringbarked; 61% pushed over	Rate for trees >7 m in height between 1967 and 1972	Harrington and Ross (1974), Field and Ross (1976)
<i>Acacia nilotica</i>	Venetia-Limpopo NR, South Africa	23.2	100% ringbarking	Accumulated mortality by 1998 since re-introduction of elephant in 1991/1994	MacGregor and O'Connor (2004)
<i>Acacia senegal</i>	Serengeti NP, Tanzania	1.6 pa	Ringbarking, crown removal, pushed over, uprooted	Rate between 1968 and 1971, elephant feeding loci sampled	Croze (1974b)
<i>Acacia seyal</i>	Kalamaloue NP, Cameroon	51	Crown removal and uprooting	Accumulated mortality until survey, mainly 1986–1991	Tchamba and Mahamat (1992)
<i>Acacia seyal</i>	Waza NP, Cameroon	6	3% uprooted, 3% pollarded	Snapshot survey	Okula and Sise (1986)
<i>Acacia tortilis</i>	Serengeti NP, Tanzania	6.3 pa	Ringbarking, crown removal, pushed over, uprooted	Rate between 1968 and 1971. Elephant feeding loci sampled	Croze (1974b)
<i>Acacia tortilis</i>	Serengeti NP, Tanzania	5	27% pollarding, 10.8% debarking, 2.1% uprooted, 1.8% pushed over	Rate 1972–1982	Ruess and Halter (1990)
<i>Acacia tortilis</i>	Lake Manyara NP, Tanzania	5.3 pa	Crown removal and ringbarking	Rate 8.3% pa between 1975 and 1979, 4% pa between 1979 and 1985; for adult trees	Mwalyosi (1987, 1990)
<i>Acacia tortilis</i>	Sengwa WRA, Zimbabwe	86	Mainly ringbarking followed by borer attack	Accumulated mortality until survey in 1973, mainly from 1965	Anderson and Walker (1974)
<i>Acacia tortilis</i>	Venetia-Limpopo NR, South Africa	15.2 pa	50% pushed over, 35.7% pollarded, 7.1% uprooted, 7.1% crown removal	Rate 1996–2000 following re-introduction. Debarked trees died from subsequent pollarding or uprooting	MacGregor and O'Connor (2004)
<i>Acacia tortilis</i>	Tsavo NP, Kenya	15.8 pa	Not described	Rate of trees between 1970 and 1974, coincided with drought	Leuthold (1977)
<i>Acacia xanthophloea</i>	Serengeti NP, Tanzania	3.9 pa	Ringbarking, crown removal, pushed over, uprooted	Rate between 1968 and 1971. Elephant feeding loci sampled	Croze (1974b)
<i>Adansonia digitata</i>	Ruaha NP, Tanzania	2.7 pa	Debarking and gouging	Rate between 1976 and 1982, thereafter minimal following poaching of bulls	Barnes et al. (1994)
<i>Adansonia digitata</i>	Mana Pools NP, Zimbabwe	7.25 pa	Debarking and gouging	Rate 1983–1987 close to permanent water, 0% far from water	Swanepoel (1993)
<i>Adansonia digitata</i>	Lake Manyara NP, Tanzania	1.1 pa	Debarking and gouging	Rate for 1981, was 0% in 1969; smaller trees	Weyerhauser (1985)
<i>Adenia spinosa</i>	Venetia-Limpopo NR, South Africa	72.8 in 5 years	Detachment of plant at ground level, gouging	Mortality preceding 2002 following re-introduction in 1991	O'Connor, unpublished data
<i>Aloe marlothii</i>	Songimvelo GR, South Africa	2.9 pa	Crowning 62.7%; pollarding 22.7%; uprooted 18.8%	Mortality over 8 years since re-introduction of elephant (0.18 km ⁻²) in 1992/1993	Steyn (2003)
<i>Androstachys johnsonii</i>	Gonarezhou NP, Zimbabwe	1.4 pa	Not specified	Rate between 1970 and 1983	Tafangenyasha (1997)
<i>Balanites aegyptiaca</i>	Sengwa WRA, Zimbabwe	50	Crown removal and pollarding	Accumulated mortality until survey in 1973, mainly from 1965	Anderson and Walker (1974)
<i>Balanites aegyptiaca</i>	Kalamaloue NP, Cameroon	48	Crown removal and uprooting	Accumulated mortality until survey, mainly 1986–1991	Tchamba and Mahamat (1992)
<i>Brachystegia boehmii</i>	Chizarira NP, Zimbabwe	18.3 pa	62% felled; 33% ringbarked; 5% uprooted	Mean mortality for 1972/3	Thomson (1975)
<i>Brachystegia boehmii</i>	Gwaai FR, Zimbabwe	2	Small pushed over, large ringbarked	Accumulated mortality up until survey	Campbell et al. (1996)

(continued on next page)

Table 2 – continued

Species	Reserve	Mortality (%)	Manner of mortality	Comment	Source
<i>Brachystegia boehmii</i>	Sengwa GR, Zimbabwe	47	Ringbarking pronounced, pollarding and crown removal	Accumulated mortality until survey in 1973, mainly from 1965	Anderson and Walker (1974)
<i>Brachystegia glaucescens</i>	Gonarezhou NP, Zimbabwe	1.7 pa	Not described	Rate between 1970 and 1983	Tafangenyasha (1997)
<i>Colophospermum mopane</i>	Gonarezhou NP, Zimbabwe	4.7 pa	Not described	Rate between 1970 and 1983	Tafangenyasha (1997)
<i>Colophospermum mopane</i>	Luangwa Valley NP, Zambia	~8 pa	50% felled, 50% ringbarked	4% felled per year, estimates the same ringbarked	Caughley (1976)
<i>Colophospermum mopane</i>	Luangwa NP, Zambia	1.4 pa	Uprooted, ringbarked, pollarded	Rate between 1982 and 1986; adults on east bank of river	Lewis (1991)
<i>Colophospermum mopane</i>	Luangwa NP, Zambia	0.5 pa	58% crown removal, 42% uprooting/pushed over	Rate between 1982 and 1986; coppice individuals	Lewis (1991)
<i>Colophospermum mopane</i>	Sengwa WRA, Zimbabwe	22	Mainly pollarding, ringbarking minor	Accumulated mortality until survey in 1973, mainly from 1965	Anderson and Walker (1974)
<i>Combretum aculeatum</i>	Kalamaloue NP, Cameroon	60	Crown removal and uprooting	Accumulated mortality until survey, mainly 1986–1991	Tchamba and Mahamat (1992)
<i>Commiphora</i> spp.	Tsavo NP, Kenya	24 pa	Not described	Rate of trees between 1970 and 1974, coincides with drought (96% overall)	Leuthold (1977)
<i>Commiphora ugogensis</i>	Ruaha NP, Tanzania	8.2 pa	Mostly pushed over	Rate between 1971 and 1982	Barnes (1985)
<i>Cussonia spicata</i>	Songimvelo GR, South Africa	5.6 pa	Debarking 55.6%; pollarding 19.8%; uprooted 16.7%	Rate since re-introduction (0.18 km^{-2}) in 1992/1993	Steyn (2003)
<i>Delonix elata</i>	Tsavo NP, Kenya	12.4 pa	Not described	Rate of trees between 1970 and 1974, coincides with drought	Leuthold (1977)
<i>Euphorbia candelabrum</i>	Murchison Falls NP, Uganda	5.7 pa	Mainly ringbarking	Rate between 1968 and 1973	Eltringham (1980)
<i>Faidherbia (Acacia) albida</i>	Ruaha NP, Tanzania	6.67	Mostly ringbarked	Rate between 1971 and 1984	Barnes (1983a,b)
<i>Faidherbia (Acacia) albida</i>	Namib desert, Namibia	2.3	Ringbarking	Accumulated mortality up until time of survey	Viljoen and Bothma (1990)
<i>Monotes glaber</i>	Sengwa GR, Zimbabwe	29	Mainly crown removal and pollarding, some uprooting and ringbarking	Accumulated mortality until survey in 1973, mainly from 1965	Anderson and Walker (1974)
<i>Piliostigma reticulatum</i>	Kalamaloue NP, Cameroon	39	Crown removal and uprooting	Accumulated mortality until survey, mainly 1986–1991	Tchamba and Mahamat (1992)
<i>Pterocarpus angolensis</i>	Gwaai FR, Zimbabwe	13	Small uprooted, large ringbarked	Accumulated mortality up until survey	Campbell et al. (1996)
<i>Pterocarpus angolensis</i>	Songimvelo GR, South Africa	0.96	Ringbarking	Mortality over 8 years since re-introduction of elephant (0.18 km^{-2}) in 1992/3	Steyn and Stalmans (2001)
<i>Sclerocarya birrea</i>	Kruger NP, South Africa	2.3	Ringbarking and pushed over (not distinguished)	Rate between 1973 and 1979 for high elephant density, low tree density region	Coetzee et al. (1979)

Tchamba and Mahamat, 1992; Kabigumila, 1993; Höft and Höft, 1995; Tchamba, 1995; Campbell et al., 1996; Holdo, 2003) and uprooting of regenerating individuals (<1 m high) can be severe (Vesey-Fitzgerald, 1973; Anderson and Walker, 1974; Barnes, 1983a; Tchamba and Mahamat, 1992; Kabigumila, 1993; Dublin, 1995; Tchamba, 1995; Western and Maitumo, 2004; Birkett and Stevens-Wood, 2005). Regeneration may also be indirectly impaired by elephant trampling when a species grows in association with a highly selected species (Lawes and Chapman, 2006).

Elephant exhibit strong species selection (Guy, 1976; Jachmann and Bell, 1985; Kalemera, 1989; Viljoen, 1989; Ruess and Halter, 1990; Tchamba, 1995; Smallie and O'Connor, 2000; Holdo, 2003), but selected species may not be used in a similar manner (Van Wyk and Fairall, 1969). The manner in which an elephant may use a plant and the propensity of that plant's growth response to compensate for utilisation should determine whether the plant survives. The manner in which a plant is used depends, in part, on its attributes. For woody trees, pollarding and uprooting result from an elephant pushing against the main stem of a tree to gain access to, and enable rapid harvesting of crown foliage and fruit, or to expose roots (Croze, 1974a; Jachmann and Bell, 1985; Clegg, unpublished data). (Proposals that bull elephants push over trees for display (Guy, 1976; Hiscocks, 1999) are equivocal (Croze, 1974a, p. 25).) Nutrient content of foliage, lack of toxic compounds, and availability of foliage during the dry season may all influence a tree's attractiveness to elephant (Jachmann and Bell, 1985; Holdo, 2003). Whether the stem snaps or the tree uproots depends primarily on stem size, strength of stem wood, presence of a taproot, tensile strength of roots, and inertness of the soil matrix. When pushed, a hardwood stem in soft or sandy ground is likely to uproot rather than be pollarded; bole diameter sets a limit to which stems can be broken for any given wood density. A hardwood stem in firm ground will snap or uproot depending on the strength of the root system (*Balanites aegyptiaca* (Croze, 1974b)) or presence of a taproot (Guy, 1976; Eltringham, 1982). Root excavation is more easily achieved in sandy substrates than in heavy clay soils, hence species growing in sandy soils are more likely to be dug up (e.g. *Combretum* species (Van Wyk and Fairall, 1969; Hiscocks, 1999)).

Species vary considerably in the degree to which they may be debarked depending on their attributes and growth strategies, with toxic compounds in the bark preventing debarking of some species (Sheil and Salim, 2004). Debarking of potentially utilisable species depends on the ease with which bark can be separated from the stem (resistance), whilst complete ringbarking depends further on the structure and number of main stems (avoidance). Species in a semi-arid savanna varied from those with a clean bole and stringy bark that were easily ringbarked, single boles whose bark has to be chiselled off in small blocks that were eventually ringbarked, multi-stemmed species with stringy bark that were easily debarked but were protected from ringbarking on the inside of stems, and a fine bark structure that limited debarking (O'Connor, unpublished data). Only a sliver of bark need remain for a tree to survive (Coetzee et al., 1979).

Mortality depends further on the ability of a plant to regrow following pollarding, debarking or uprooting. Species

whose adults lack sufficient coppicing ability (bud activation and shoot regrowth vigour) would eventually die as a result of severe elephant utilisation. Coppicing ability is determined by the availability of buds around the stem base below the common height of pollarding or ringbarking by elephant (1–2 m), and depends on species identity and tree age (Abbot and Loworeb, 1998; Luoga et al., 2004). Adults of some species such as *Colophospermum mopane* have a strong coppicing ability (Lewis, 1991; Ben-Shahar, 1996; Styles and Skinner, 2000), others a weak ability (e.g. *Acacia tortilis*, MacGregor and O'Connor, 2004), and others do not coppice (e.g. *Commiphora merkerii*, O'Connor, unpublished data). Consequently in response to elephant impact, *C. mopane* usually survives with the exception of large individuals, the weak coppice growth of *A. tortilis* usually dies within a year, and *C. merkerii* dies soon after being pollarded. Strong coppicing ability (e.g. *Brachystegia boehmii*) can ensure persistence following elimination of adult woodlands (Thomson, 1975; Lock, 1977; Cumming, 1981b).

Whether a population with elevated adult mortality incurred by elephant would tend toward extirpation would depend on whether seedling regeneration and recruitment are sufficient for maintaining a population. Risk of extirpation is expected to be greater for a population in which regeneration is an infrequent event involving few seedlings compared to ongoing regeneration of large numbers of seedlings. In support, most *Acacia* species heavily impacted by elephant (Table 2) have persisted on account of their regeneration ability (Croze, 1974b; Leuthold, 1977; Vesey-Fitzgerald, 1973, 1974; Pellew, 1983; Mwalyosi, 1990; Lock, 1993; Dublin, 1995; Western and Maitumo, 2004). Rainfall, fire, and other herbivores can complement elephant in limiting recruitment and regeneration to an extent that depends on species identity and habitat. Forest or woodland has been converted to grassland in moist or mesic regions as a result of the combined impact of fire, elephant and other herbivores (Buechner and Dawkins, 1961; Laws et al., 1975; Pellew, 1983; Dublin et al., 1990; Starfield et al., 1993), but a similar role of fire has not been recorded for semi-arid systems where its impact is presumably too weak. For species in which seedling regeneration occurs mainly during a 'wet' year (O'Connor, 1995), infrequent regeneration may occur (Jeltsch et al., 1996, 1997). Regeneration of a species restricted to a small habitat selected by a small-bodied, herd-forming browser may be limited to infrequent events when the browser species experiences population die-off from disease (Prins and Van der Jeugd, 1993).

It is speculated that some long-lived icon species are under increased threat of local extirpation because of infrequent regeneration related to climatic cycles. Climate over the Holocene has alternated between century-long epochs of wetter, warmer and drier, cooler conditions that differed in mean annual rainfall by up to 200 mm (Huffman, 1996; Tyson and Partridge, 2000; Gillson, 2004; Holmgren and Öberg, 2006). The extended dry 'Little Ice Age' (1300–1800 AD) was interrupted by short, intensely wet phases (Zawada, 2000; Lamb et al., 2003). Based on uniform population size structures, it is suggested that regeneration of species that can live for centuries or a millennium, such as baobab *Adansonia digitata* (Swart, 1963) or leadwood *Combretum imberbe* (Vogel and Fuls, 2005),

occurred mainly during wet epochs for populations toward the drier end of their geographical distribution (e.g. O'Connor, 2001). High rainfall epochs have occurred with sufficient frequency for populations to persist with punctuated regeneration every few centuries. Such a species would be exposed to an increased threat of local extirpation if elephant killed off the adult population that could not be compensated by regeneration until the next wet epoch, and the species lacked long-lived seeds and is poorly dispersed. In support, the characteristically mesic species *Sclerocarya birrea* (Coates Palgrave, 1983) has been extirpated by elephant from the semi-arid Tuli Block Reserve in Botswana but an abundant adult population with no regeneration occurred on the adjacent Venetia-Limpopo Nature Reserve prior to recent re-introduction of elephant after an absence of a century (Table 1). Future re-establishment during a wet epoch will require dispersal on account of its short-lived seeds.

Impacts on a population usually occur in a meta-population context in which local extirpations can be compensated by recolonisation (Hanski, 1999). The threat of local extirpation at a reserve level is heightened for species with a limited meta-population structure, specifically narrow habitat specificity and restricted geographic distribution, an apparently apt profile for a number of species listed in Table 1. Such population characteristics of a species selected by elephant could predispose its population to rapid elimination through heightened mortality. Recolonisation following extirpation becomes dependent on the effectiveness of dispersal, which is a function of propagule supply, efficacy of dispersal agent, ease of seedling establishment and of growth. Species with poor reproductive output (characteristically a few, large seeds) and limited dispersal distances are particularly vulnerable (O'Connor, 1991). For potentially vulnerable large-seeded species, those with fleshy fruits (e.g. *S. birrea*, *Commiphora* spp.) should be dispersed for greater distances by large, wide-ranging mammals including elephant (Lewis, 1987; Babweteera et al., 2007) or birds, respectively, than wind would disperse those with large, winged pods (e.g. *Pterocarpus angolensis*) (Table 1).

In summary, elephant may cause extirpation of a population if (i) they select for a species whose attributes predispose it to pollarding, uprooting or ringbarking; (ii) the species lacks an adequate coppicing response hence mortality results; (iii) regeneration and recruitment cannot compensate for elevated mortality because of the impact of elephant, fire, drought, or herbivory; and (iv) the species has a restricted distribution; and (v) recolonisation is constrained by poor dispersal ability of a limited number of seeds.

4. Local extirpation in relation to reserve or ecosystem characteristics

4.1. Introduction

Plant species threatened with local extirpation by elephant have previously co-existed with this mega-herbivore for millennia. This section proposes that changes in environment or in key characteristics of some ecosystems or reserves may have increased the threat of local extirpation to these species.

4.2. System configuration: probability of encounter

An increase in elephant-related mortality of trees requires that elephant encounter trees, the probability of which depends on elephant density, size of the system and characteristics of its environment. The probability of an elephant–tree encounter can vary from zero for a tree growing in an inaccessible location to almost certainty for a tree located where elephant pass daily. Probability of encounter is influenced by both frequency and duration of visits, and resultant impact on plants is influenced by seasonal timing of visits. Persistence of a woody species should be ensured if it occurs partly in spatial refuges from elephant. A spatial refuge is defined as an area which decreases the probability of encounter between elephant and a plant. A refuge may be absolute such that elephant cannot physically access it, or it may be partial in which elephant are less likely to access the site. An absolute refuge can be provided by inaccessible topography such as cliffs (e.g. Weyerhauser, 1985), but they are of limited occurrence. Rugged but accessible terrain is likely to provide a partial refuge where there it is surrounded by gentle terrain with forage because elephant prefer utilising less difficult terrain (Thomson, 1975; Nelleman et al., 2002). Community composition may influence the degree of partial refuge afforded a species. A vulnerable species within a poor foraging habitat is less likely to be encountered than one in the midst of elephant cornucopia because elephant show strong selection for plant communities (Van Wyk and Fairall, 1969; Field and Laws, 1971; Williamson, 1975a; Viljoen, 1989).

4.3. System configuration: reserve size and foraging area

In open systems, elephant commonly exhibit seasonal movements or even long migrations in response to changes in water and food availability that results in certain habitats being used only on a seasonal basis (Buss, 1961; Buss and Savidge, 1966; Laws et al., 1975; Williamson, 1975a; Leuthold and Sale, 1973; Ross et al., 1976; Eltringham, 1977; Dunham, 1986; Viljoen, 1989; Thouless, 1995; Leggett et al., 2003). Patterns of movement and habitat selection differ between bulls and cow herds (Jarman, 1972; Stokke and du Toit, 2002). Compression of elephant into reserves or fixing of boundaries could deprive elephant of access to a key seasonal habitat that would result in an extended period of occupation of selected habitats within a reserve. This in turn would increase the probability of encounter of elephant with selected tree species and thus tree mortality.

4.4. System configuration: surface water

The most important spatial refuge from elephant is distance from water. Elephant drink on a near daily basis which restricts foraging to within about 15 km from water (Conybeare, 2004). Plants occurring at greater than the maximum distance enjoy an absolute refuge. Plants occurring toward the potential foraging range limit are afforded a partial refuge because they are less likely to be encountered as a result of a greater searching area and energetic influences on travelling distance. Limits on distance travelled from water differs between bulls and cow-calf herds (Stokke and du Toit, 2002) as

expected on the basis of energetic limitations related to body size, with young calves limited to about 5 km (Young, 1970).

Absolute and partial refugia dependent on distance from water have been consistently eroded in African reserves through provision of artificial water points (Western, 1975; Owen-Smith, 1996). These have been created to compensate for loss of access to traditional watering areas, to ensure provision of water for all mammals during drought years, and to increase the foraging area available to water-dependent animals (Van Wyk and Fairall, 1969; Cumming, 1981a). Reserves derived from livestock ranches inherited a uniform distribution of water that served to maximise available range. The net result is that no point may be more than a few kilometres from water, former absolute refuges become partial refuges, and probability of encounter between elephant and trees within former partial refuges increases. This effect on accessibility has been dramatic even in large reserves. In Kruger NP (19,000 km²), addition of 310 water points resulted in 96% of the reserve being within 8 km of water (Redfern et al., 2005); artificial water points provided between 1936 and 1980 increased the area of Hwange NP available to elephant from 35% to 75% (Cumming, 1981a).

Increased access of elephant to previously waterless habitats will alter the frequency, timing and duration of utilisation of woody vegetation. These habitats would previously have been utilised occasionally by elephant during the wet season when ephemeral water was available (Williamson, 1975a; Conybeare, 2004). Browsing of foliage would have been the expected pattern of utilisation, but continued utilisation by elephant exposes these species to an increased frequency of debarking and uprooting during the dry season. Containing the threat of local extirpation is therefore closely dependent on maintaining the strength of partial and absolute spatial refugia based on distance from water. Configuration of water availability is one of the few actions available to management through which impact on woody species in habitats not historically accustomed to elephant utilisation can be reduced or avoided.

4.5. Surface water availability: weakening of population regulation

Density-dependent effects usually manifest in elephant populations when numbers increase and resources decline as an increased age of first breeding, a longer inter-calving period (conception frequency), and increased calf and juvenile mortality (Buss and Savidge, 1966; Laws et al., 1975; Laws, 1981), of which neonatal mortality has the strongest influence on the rate of population growth (Hanks and McIntosh, 1973). Density-dependent effects are heightened during drought events, when entire cohorts of calves can be killed (Corfield, 1973; Dudley et al., 2001). These effects are realised through local density determined by available habitat in relation to water (Owen-Smith, 1996). An increase in available water will increase available habitat and thereby increase population size. Conversely, removing artificial water will promote crowding around remaining natural water sources, creating a high local density that will intensify density-dependent effects resulting from depletion of vegetation resources, loss of feeding time, and physiological drains from increased energy expenditure

on travel for foraging (Owen-Smith, 1988). Vegetation near perennial water will become heavily impacted. Plant species that can tolerate, resist, or avoid impact should persist, which may reflect the situation that once naturally prevailed assuming high elephant numbers existed before ivory hunting during the 19th century. The nature of these strategies for species which are restricted to riparian habitats (e.g. Dunham, 1989a,b; Hughes, 1990; O'Connor, 2001) has yet to be elucidated.

4.6. Historical vegetation change

Anthropogenic changes in vegetation over the past century need to be accounted for when assessing elephant impact. Degradation of grassland would result in increased utilisation and mortality of the woody component because herbaceous material is the mainstay of an elephant's summer diet, especially bulls ('Elephant foraging ecology'). Degradation would deprive elephant of adequate grazing during summer as it is characterised by compositional deterioration of a sward from palatable, broad-leaved grasses to coarse, wiry grasses (O'Connor, 1985) not selected by elephant, and by bush encroachment (Van Vegten, 1983; Roques et al., 2001) that depresses grass production (Smit et al., 1996). These patterns have been most pronounced in semi-arid rather than in mesic environments. Small and medium-sized reserves can be degraded by severe wildlife grazing pressure arising, in part, through provision of artificial water (Walker et al., 1987). Many private wildlife reserves in southern Africa are derived from degraded livestock areas whose poor grazing during summer can force elephant to subsist year-round on woody vegetation (e.g. Smallie and O'Connor, 2000).

Semi-arid regions experience a greater frequency of droughts of greater duration than mesic areas, characterised by reduced grass production (Dye and Spear, 1982; O'Connor et al., 2001) but stable browse production (Kelly and Walker, 1976) although browse leaf fall occurs earlier (Dekker and Smit, 1996). Drought years would therefore produce less herbaceous material during the growing season for elephant, resulting in them using woody plants earlier, and for longer, in the dry season. Degraded semi-arid systems are therefore predicted to be vulnerable to local extirpation of certain woody species because elephant would have to subsist almost year-long on woody material. Tuli GR is a degraded semi-arid reserve (Walker et al., 1987) in which a conspicuous number of woody species have been extirpated (Table 1).

Riparian and wetland habitats can serve as key habitats for elephant by providing forage of adequate quality at the height of the dry season (Buss, 1961; Buss and Savidge, 1966; Jarman, 1972; Wyatt and Eltringham, 1974; Western and Lindsay, 1984; Lewis, 1986; Tchamba and Mahamat, 1992; Kalempera, 1989; Kabigumila, 1993). Catchment degradation, water extraction and impoundments have impacted on the hydrological functioning of rivers and consequent ecological functioning of associated habitats (Hughes, 1988, 1990). Impoundments result in water and sediment retention, which attenuates floods and deprives downstream floodplains and river banks of water and sediment recharge that reduces production and growing period, increases bank erosion, elevates tree mortality, and desiccates wetlands (Dunham, 1989a,b, 1990;

O'Connor, 2001). Catchment degradation results in increased summer flows and reduced winter flows that increase erosion, hence desiccation of floodplains and wetlands (Van Wijngaarden, 1985). Foraging opportunities of elephant are therefore compromised at a critical time of the year, which should force them to rely on dryland browse earlier in the season and for a greater duration. Consistent with this expectation, elephant impact on dryland woody plants increased considerably as a result of loss of floodplain through upstream irrigation in Kalamaloue National Park, Cameroon (Tchamba and Mahamat, 1992), which formerly served as a key dry season foraging area for elephant (Tchamba, 1995).

There has been an extended period during which woody vegetation changed in the absence or lessened impact of elephant and other herbivores (Dublin, 1995) owing to depletion of elephant by hunting in the 19th century (Selous, 1972; Croze, 1974a; Struthers, 1991; Whyte, 2001), impact of the rinderpest pandemic (elephant were not affected) during the late 19th century (Prins and Van der Jeugd, 1993), and former use of many smaller reserves for livestock. Species which expanded their habitat during this period (e.g. hills onto plains) are expected to experience high impact as elephant populations recover and reverse vegetation toward a previous state.

4.7. Elimination of predation

Rate of population growth is sensitive to the population mortality schedule (Hanks and McIntosh, 1973). Humans and lions have historically been the most effective predators of elephant. Elephant populations continue to increase in reserves lacking poaching or culling (Conybeare, 2004). It is proposed that the absence of human hunting from many reserves coupled with the manner in which an increased availability of water has compromised predation by lion by reducing stress on elephant calves and juveniles has contributed to current population growth rates of elephant.

Lion prey upon elephant calves and juveniles, especially those weakened by travel (Owen-Smith, 1988; Ruggiero, 1991; Joubert, 2006). Calves are expected to be well protected from predation by a cow herd when foraging is restricted to within a few kilometres of water (Western, 1975; Stokke and du Toit, 2002) because energetic costs are reduced and body condition of even the youngest is maintained. Foraging range from water of cow herds would increase during the dry season, with increasing local density of elephant, and during drought years. The cost of this increased energy demand on body condition is in relation to body size. Calves expend proportionately a greater amount of energy on travel than adults, and therefore become considerably weakened and may die during drought conditions (Owen-Smith, 1988). Calves would struggle to keep up with the herd and become more vulnerable to predation by lion, hyaena or wild dog, which select for weakened individuals (Kruuk, 1972; Schaller, 1972; Poché, 1974). The impact of predation on population growth may not be substantial because predated calves may have succumbed anyway. Whatever its impact, it is less likely to be realised in a system in which foraging distances have been reduced through provision of water.

African elephant have been hunted by humans for at least 4000 years (Spinage, 1994) and proboscideans for ~1.8 million years since range expansion of *Homo* began (Surovell et al., 2005). Pre-colonial hunting apparently targeted mostly adults or sub-adults for meat and ivory whether using indiscriminate pit-traps (Baldwin, 1967) or involving specialist elephant hunters (Holman, 1967; Thomas, 1970). Humans also created partial refuges for plants because elephant apparently avoid areas of human settlement, as indicated by the diaries of early European hunters (Baldwin, 1967; Selous, 1972; Barnes, 1983b; Delegorgue, 1990; Struthers, 1991).

Lion predation of calves and juveniles and human predation of adults and sub-adults could complement density-dependent regulation of elephant numbers, which needs to be examined with a model that accommodates elephant energetics on an age- and sex-specific basis in relation to foraging distance from water, elephant density, and a variable supply of forage in relation to climatic variability. In the absence of such insight, it is conjectured that reinstating predation processes through configuration of water availability or through simulation where lion are now absent could contribute to dampening elephant population growth rates.

5. Implications for management and decision-making

Comment is offered on only those management issues directly related to the paper's subject matter. A key challenge for management has been to define a reserve's carrying capacity for elephant, but this concept is under attack (Gillson and Lindsay, 2003). We consider that elephant numbers should not be the focus of attention for containing elephant impact. First, the conventional notion of carrying capacity addresses an inappropriate issue. It is concerned with the number of herbivores that can be sustained, not the number that will ensure persistence of threatened woody species, loss of which is unlikely to affect the size of an elephant population. Second, impact on woody vegetation differs between bulls and cows, and between juveniles and adults. Third, determining the density of elephant appropriate for ensuring persistence of threatened plant species is not practicable. It would depend on system configuration, reserve area, climate, water availability, attributes of species, nature of their utilisation by elephant, and would not be a fixed value on account of climatic variability. Finally, informal review suggests that many plant species under threat of local extirpation have become more exposed to elephant utilisation as a result of provision of artificial water or restricted movement of elephant.

We propose that management should concentrate on key processes influencing potential extirpation of woody species. Alteration of reserve boundaries to ensure continued access to key habitats is highly desirable but difficult to achieve (e.g. Western, 2002). Systems should be configured to ensure that partial and absolute spatial refuges from elephant are maximised, and that density-dependent processes controlling elephant numbers are reinforced. Limiting the distribution of water to historical sources, where practicable, is the most pragmatic means of achieving both. Vegetation in the vicinity of remaining water will be transformed (Van Wyk

and Fairall, 1969; McShane, 1987; Thrash et al., 1991; Tafange-nyasha, 1997) but the total area impacted is reduced. This inevitable concentration of impact in the vicinity of historical water sources would probably have prevailed in the past (Skarpe et al., 2004). Increased local elephant density around water and consequent increased foraging distance and weakening of calves should intensify density-dependent effects (Buss and Savidge, 1966; Laws et al., 1975; Williamson, 1975a; Laws, 1981; Owen-Smith, 1988; Ruggiero, 1992), and facilitate predation (Ruggiero, 1991). Together these should depress the rate of population growth and limit elephant densities (Hanks and McIntosh, 1973). In addition, simulated predation is a common management practice for some smaller reserves where large predators are lacking, and could be considered for elephant.

The content of this paper provides the following prediction of the conditions that render a species most vulnerable to extirpation in a small reserve: (a) terrain lacks topographic refuges; (b) there are no absolute and only weak partial refuges from elephant because distance from water is not a foraging constraint; (c) woody species of concern have limited distributions and are restricted to selected foraging habitats; (d) reserve is located in a semi-arid region that experiences variable grass production, hence heightened utilisation of woody material occurs; (e) reserve is a degraded semi-arid savanna in which suitable grass is infrequently available, hence woody species constitute the mainstay of the diet; (f) the species is highly selected, (g) frequently subjected to pollarding or complete ringbarking, (h) lacks a coppicing ability so that mortality usually results from pollarding or ringbarking, (i) regenerates infrequently and usually in small numbers; (j) grows slowly so that adults are not easily recruited, and (k) is long-lived, regenerating only during wetter epochs and not currently.

Extirpation of woody plants appears a reality for many smaller reserves (Table 1), bringing into question the size and state of reserves into which elephant are re-introduced if local extirpation of plant species is to be avoided. An alternative is to accept extirpation of a species within a small reserve but to safeguard their persistence at a regional scale by maintaining areas under alternative land uses (e.g. live-stock ranching) which impact less on woody vegetation.

6. Conclusion

We have presented a mechanistic hypothesis to account for the possible local extirpation of selected woody species by elephant that scales from digestive physiology through to ecosystem or reserve characteristics. This hypothesis is equally applicable to the impact of elephant on woodlands on which certain animal species are dependent. It awaits theoretical and empirical development and heuristic application to individual cases for identifying inconsistencies, contradictions, and necessary expansions. It is offered as a first step toward formulating an approach for mitigation of elephant impact in large and medium-sized reserves or for identifying small reserves where it seems inevitable that local extirpation of certain plant species will occur. Management tools are limited, but configuration of water supply provides a starting template.

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