Keystone megaherbivore hypotheses – white elephants?

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Abstract

Major vegetation changes at the end of the Pleistocene are often concomitant with the extinction of most of the world's megafauna. However, human hunting, and not climate appears to have been the main driving force behind this pattern of extinction. This has led to the suggestion that megaherbivores were the keystone controllers of vegetation structure and composition during the Plesitocene, and that their presence may have allowed for a greater biodiversity of smaller herbivores. The Hluhluwe iMfolozi Park in South Africa provides a good test case for the predictions made by keystone megafauna hypotheses as elephants were only re-introduced to the park in 1981 after a century's absence. We tested the predictions that elephants as megaherbivores would promote faster-growing, more palatable woody species, that they cause a decrease in overall vegetation size making woody vegetation more accessible to smaller herbivores, and that elephants should open up closed woodlands and forests. Our findings suggest that elephants cause an increase mostly in spinescent and chemically well-defended woody species. They do appear to reduce the overall height of vegetation, however this is most marked in species they highly favour. Elephants avoid densely wooded areas and forests and the majority of their impact occurs in already open woodlands. They thus appear to contribute to the formation of more uniform grasslands and forests, and not to the creation of a mosaic of trees and grasslands.

Introduction:

Most of the world's megafauna, being those animals 1000 kg and heavier, went extinct over a period from about 100 000 to 10 000 years ago (Owen-Smith 1989, Barnosky *et al.* 2004, Miller *et al.* 2005). Africa and tropical Asia were the only regions to be largely spared from this almost exclusive elimination of larger animals (Owen-Smith 1989, Barnosky *et al.* 2004). These extinctions have been attributed to climate change at the beginning of the Holocene, predation of the megafauna by humans after the arrival of people on new continents, or a combination of both (Choquenot & Bowman 1998, Kerr 2003, Barnosky *et al.* 2004, Brook & Bowman 2004, Johnson 2005, Miller *et al.* 2005). Current evidence seems to suggest that human overkill of the megafauna was largely responsible for the extinction of these animals, although the effects of climate change cannot be ignored (Alroy 2001, Kerr 2003, Barnosky *et al.* 2004, Brook & Bowman 2004). Often concurrent with the extinction of the megafauna were major changes in vegetation (Zimov *et al.* 1995, Lambert & Holling 1998, Zimov 2005). This has led to the suggestion that the megafauna of the world controlled vegetation structure and composition (Owen-Smith 1987, 1989 & 1999, Zimov 2005, Johnson 2005).

Arising from this assumption is the "Keystone Megaherbivore hypothesis" of Owen-Smith (1987, 1988, 1989 & 1999). This predicts that megafauna would have had far-reaching effects on vegetation structure and composition, creating "open parklike woodlands and mosaic grasslands" by the opening up of woodlands and the creation of gaps in forests. The hypothesis further predicts that this would have positively affected populations of smaller herbivores by promoting faster-growing, less chemically well-defended vegetation that was more readily accessible to these smaller herbivores.

Africa is the only continent to have been largely unscathed by megafaunal extinctions (Owen-Smith 1987, 1989 & 1999, Barnosky *et al.* 2004). Of the African megafauna, elephants are probably the species most often associated with major changes in vegetation structure and composition (van Jachmann & Croes 1991, Ben-Shahar 1998, and numerous others) and should therefore be the best candidate for testing predictions of megaherbivores as major controllers of

vegetation structure and composition, and as keystone species. The effects of elephants on vegetation can thus be examined in light of predictions made by these keystone herbivore hypotheses.

Elephants are assumed to be "supreme generalists not only in their habitat tolerance, but also in their dietary acceptance of a wide range of plant species and parts" (Owen-Smith 1987). Elephants have been found to eat 133 plant species in Sengwa, Zimbabwe, 165 species in Wankie National Park, Zimbabwe, 134 species in Lake Manyara National Park, Tanzania and over 100 species in the Kruger National Park, South Africa (Guy 1976). However, elephants are known to selectively target, and cause declines, in certain species, for example *Colophospermum mopane* (Ben-Shahar 1998), *Acacia* spp (Guy 1976, Calenge *et al.* 2002, Duffy *et al.* 2002), and *Combretum* spp. (Guy 1976). The keystone megaherbivore hypothesis predicts that faster-growing species with less chemical defences will increase in abundance as a result of megaherbivore disturbance (Owen-Smith 1987).

Elephants are known to convert woodlands to shrublands, or even to grasslands (Laws 1970, Cumming *et al.* 1997) and have been shown to have caused declines in the numbers of large trees (Croze 1974, Eckhardt *et al.* 2000). Studies, however, are contradictory in showing higher impacts either in more open areas (Beuchner & Dawkins 1961), or in more dense woodlands (Calenge *et al.* 2002). A prediction of the keystone megaherbivore hypothesis is that elephants should target more dense woodlands, and open up tree gaps in forest. This would help create the "open parklike woodlands and mosaic grasslands typical of much of North America during the Pleistocene". The extinction of megaherbivores thus is predicted to have led to "the more uniform and forests and prairie grasslands we see today" as a result of trees invading forest gaps and more frequent fires killing the trees in the "mosaic" grasslands (Owen-Smith 1987, 1988).

The suggestion that large browsers such as mastodons (*Mammut*) and gomphotheres (*Cuvieronius*) would have maintained open woodlands and created tree gaps in forests relies primarily on observations of African elephant (*Loxodonta africana*) behaviour to topple large trees (Croze 1974, Hiscocks 1999) and strip the bark off tree trunks (Hiscocks 1999, Sheil & Salim 2004).

However, African elephants may strip bark off trees and topple trees, not solely for feeding, but perhaps for unique social behaviours and/or sexual display (Guy 1976, Duffy *et al.* 2002, Midgley *et al.* 2005). Evidence for behavioural reasons to topple and bark-strip trees could prove problematic for keystone herbivore hypotheses as they are based on the premise that the extinct megafauna would have had similar effects on vegetation structure as elephants do.

When introducing the keystone megaherbivore hypothesis, Owen-Smith (1987 & 1989) suggests the Hluhluwe-iMfolozi Park as an excellent site in which to test the hypothesis. Elephants were locally extirpated here between 1850 and 1890, and only re-introduced in 1981 (Owen-Smith 1989), thus simulating the Pleistocene extinctions of megafauna in other parts of the world. In 1989, Owen-Smith stated that the effects elephants would have on the vegetation in the park would only be visible in a few decades. Almost twenty years on from then, this study was conducted to test the predictions of the keystone herbivore hypotheses using data collected in 1999 and 2003 of woody plant diversity, structure and utilisation by elephants in the Hluhluwe-iMfolozi Park. This study is unique in comparing the different types of vegetation use by elephants (branch breaking, tree toppling and bark stripping) thus allowing for more refined inferences to be made regarding the relative impact and importance of these different types of vegetation use.

Methods

Data on vegetation structure and composition were collected by Earthwatch volunteers in the Hluhluwe iMfolozi Park (HiP) in KwaZulu Natal, South Africa in both 1999 and 2003. Sampling was done in 189 ¼ ha plots in the different vegetation types of the park, with a minimum of ten plots for each vegetation type. Data collection was done according to the following method (See Fig. 1): From the zero position of the GPS coordinate of each plot, a 50 m tape was laid out in a northerly direction.

From the zero point and 2 m to the right of the tape all trees up to 2 m in height were recorded (a). If 50 trees of below 0.5 m in height were found then stopped counting these ,unless a new species found. However, all trees 0.5 to 2 m in height were still counted in (a). (b) From the zero point and 2

m to left of the tape, all trees 0.5 to 2 m high were recorded. (c) From the zero point to 10 m on either side of the tape all trees 2 to 4 m high were recorded. (d) From the zero point to 25 m on either side of tape all trees > 4 m high were recorded.

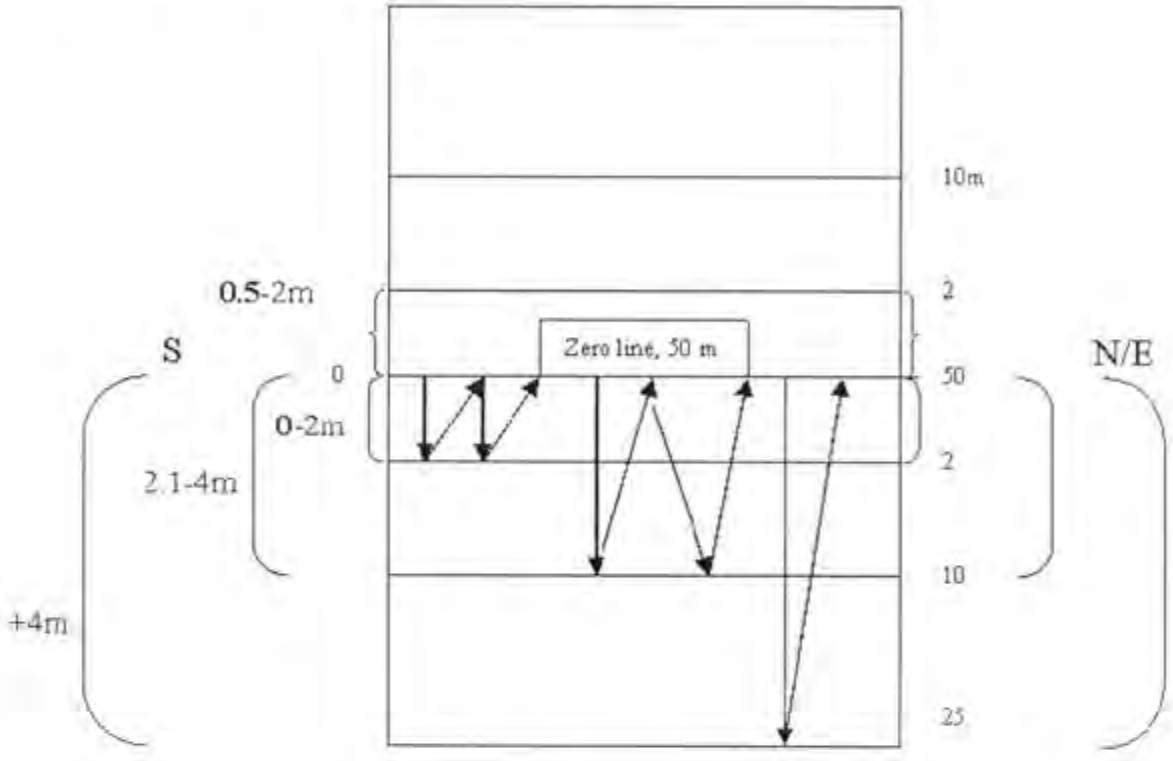

Fig. 1. Example of a plot in which sampling was conducted. Trees < 2 m high were recorded 2 m to the right of zero line, trees 0.5 to 2 m high 2 m to the left of zero line, trees 2 – 4 m in height 10 m to either side of zero line, and trees greater than 4 m 25 m to either side of zero line.

For each tree the following was recorded:

- Species
- Height. Measured vertical height unless original stem was broken or the tree was toppled over.
- Number of stems for each tree
- Diameter of stems at 0.5 m above ground level
- Elephant impacts as per Table 1.

Table 1. Types of elephant use recorded and a description of how this was done.

Elephant use type	Description
Branch breaking	Measured in categories of impact and as an estimation of the percentage of the total canopy size broken (< 5, 5-35, 36-65, 66-95, and > 95 %). Elephant breaks identified by sharp-jagged edges at point of branch breakage.
Toppling	Trees recorded as toppled if roots were exposed.
Bark stripping	Measured as the percent of total tree diameter stripped of bark and in categories of impact (< 5, 5-35, 36-65, 66-95, and > 95 %).

In order to determine elephant preference for particular species a chi-square analysis on the number of trees heavily damaged (defined as damage above 66 % impact for branch breaking and bark stripping, or simply as toppling) in each species relative to its proportional abundance was performed using STATISTICA v7.0 (StatSoft). Chi-square analyses were also performed to determine height class preference, woodland density preference, and vegetation type preference. An analysis of whether elephant use of a species was frequency dependent was performed by fitting a power function to the percent availability of a species in a plot, to its percentage use in the plot. The power function is of the form $y = Ax^B$. 'A' gives an indication of elephant preference for the species. 'B' describes the frequency dependence of utilisation (B<1: sp. targeted at low densities; B=1: sp. utilisation frequency independent; B>1: sp. targeted at high densities) (H. Fritz *pers. comm.*). Fig. 2 illustrates the different types of density dependencies as reflected by the exponent B.

B = 1 B < 1 B > 1

Fig. 2. Examples of how power functions would look like under density independent utilisation of a species (B=1), targeting at low availability (B<1), and targeting at high availability (B>1).

Results:

Species utilisation

Of the 187 woody species occurring in HiP, 138 are utilised by elephants. Most are used for browsing (136 spp.), but far fewer are bark stripped (92 spp.) or toppled (43 spp.). Of the species not utilised by branch breaking, only two had population sizes greater than 20 individuals. For species not used by bark stripping and toppling, 17 and 44 species respectively had population sizes greater than 20. However, elephants show clear preferences for certain species and how they utilise these species (Table 2 a-c). Some species are actively targeted for more than one type of use (e.g. *Acacia burkeii, Berchemia zeyheri* and *Ziziphus mucronata* for browsing and toppling, and *Acacia nilotica, Acacia robusta, Celtis africana* and *Schotia brachypetala* for browsing and bark stripping). Others are targeted mostly for browsing (*Rhus chirendensis* and *R. pentheri*), toppling (*Combretum molle*) or bark stripping (*Acacia grandicornuta*). Elephants also appear to under-utilise some very abundant species, such as *Acacia karoo, Dicrostachys cinerea, Euclea racemosa* and *Spirostachys africana*. Correlations between percentage use of species in 1999 versus 2003 show significant, albeit, fairly weak correlations for all types of use. The species which showed the biggest increases in percentage utilisation from 1999 to 2003 were mostly those identified as being favoured by elephants (Fig. 3). In contrast those species avoided by elephants showed declines in their percentage utilisation. The populations of most woody species showed remarkably similar abundances in 1999 and 2003 (Fig 4). Some species, in particular those avoided by elephants, showed marked increases (*Dichrostachys cinerea, Maytenus senegalensis* and *Spirostachys africana*). On, the other hand species actively targeted by elephants (*Acacia grandicornuta* and *Acacia nilotica*) tended to decrease in abundance.

Table 2. Species with significantly high, neutral or below expected amounts of utilisation (Chi-square test: observed versus expected number of individuals utilised per species relative to the proportion of individuals of that species (> 4m tall) to the total number of trees > 4 m tall in the park) . Species with N < 20, and less than 5 individuals utilised excluded from analysis. Average population size for 1999 and 2003 (Avg N), the observed less expected no. individuals utilised, Chi-square value and % of species utilised is given for each species.

a) Branch breaking

Plant species	Avg N	O - E	X^2	% B
Actively targeted				
Acacia burkeii	548	9	4.36	4.7
Acacia gerrardii	581	6	2.04	4.2
Acacia nilotica	1261	54	73.47	7.5
Acacia robusta	441	24	39.79	8.5
Acacia tortilis	360	11	9.94	6.1
Berchemia zeyheri	350	6	3.18	4.9
Canthium inerme	121	5	7.07	7.5
Celtis africana	138	9	17.09	9.4
Chaeciacme aristata	103	4	4.36	6.8
Hippobromus pauciflorus	123	3	1.75	5.3
Rhus chirindensis	63	4	8.19	9.6
Rhus pentheri	523	9	5.41	5.0
Scholia brachypetala	231	7	6.14	6.1
Sclerocarya birrea	152	5	4.58	6.3
Sideroxylon inerme	208	5	3.68	5.5
Strychnos madagascariensis	42	5	20.51	15.7
Ziziphus mucronata	392	18	26.52	7.8
Neutral				
Acacia grandicornuta	847	0	0.00	3.2
Combretum molle	395	0	0.02	3.0
Dombeya rotundifolia	204	0	0.00	3.2
Euclea natalensis	218	0	0.02	3.0
Under-utilised				
Acacia karoo	1414	-3	0.23	2.9
Acacia nigrescens	542	-8	3.39	1.8
Dichrostachys cinerea	2720	-62	44.69	0.9
Euclea divinorum	727	-3	0.53	2.7
Euclea racemosa	2280	-23	7.40	2.1
Kraussia floribunda	343	-3	1.02	2.2
Maytenus heterophylla	626	-9	4.35	1.7
Maytenus senegalensis	788	-19	14.36	0.8
Micrococca capensis	303	-5	2.18	1.7
Plectronella armata	331	-3	0.83	2.3
Spirostachys africana	2477	-43	23.95	1.4

b) Toppling

Plant species	Avg N	O - E	X^2	% T
Actively targeted				
Acacia burkeii	548	4	2	4.3
Berchemia zeyheri	350	10	22	3.3
Combretum molle	395	4	3	2.3
Ziziphus mucronata	392	8	11	2.0
Neutral				
Acacia robusta	441	2	0	2.4
Acacia tortilis	360	2	1	1.9
Rhus pentheri	523	-1	0	1.7
Sideroxylon inerme	208	2	2	1.1
Under-utilised				
Acacia nilotica	1261	-3	0	1.1
Acacia gerrardii	581	-3	1	0.9
Euclea racemosa	2280	-25	20	0.3

c) Bark stripping

Plant species	Avg N	O - E	X^2	% S
Actively targeted				
Acacia grandicornuta	847	33	61.60	6.0
Acacia nilotica	1261	32	39.60	4.7
Acacia robusta	441	18	35.69	6.2
Celtis africana	138	4	5.76	5.1
Schotia brachypetala	231	12	30.25	7.4
Neutral				
Acacia gerrardii	581	0	0.01	2.2
Berchemia zeyheri	350	1	0.05	2.3
Under-utilised				
Acacia burkeii	548	-6	3.16	1.0
Acacia nigrescens	5412	-3	1.02	1.5
Dichrostachys cinerea	2720	-49	42.41	0.3
Spirostachys africana	2477	-42	34.09	0.4

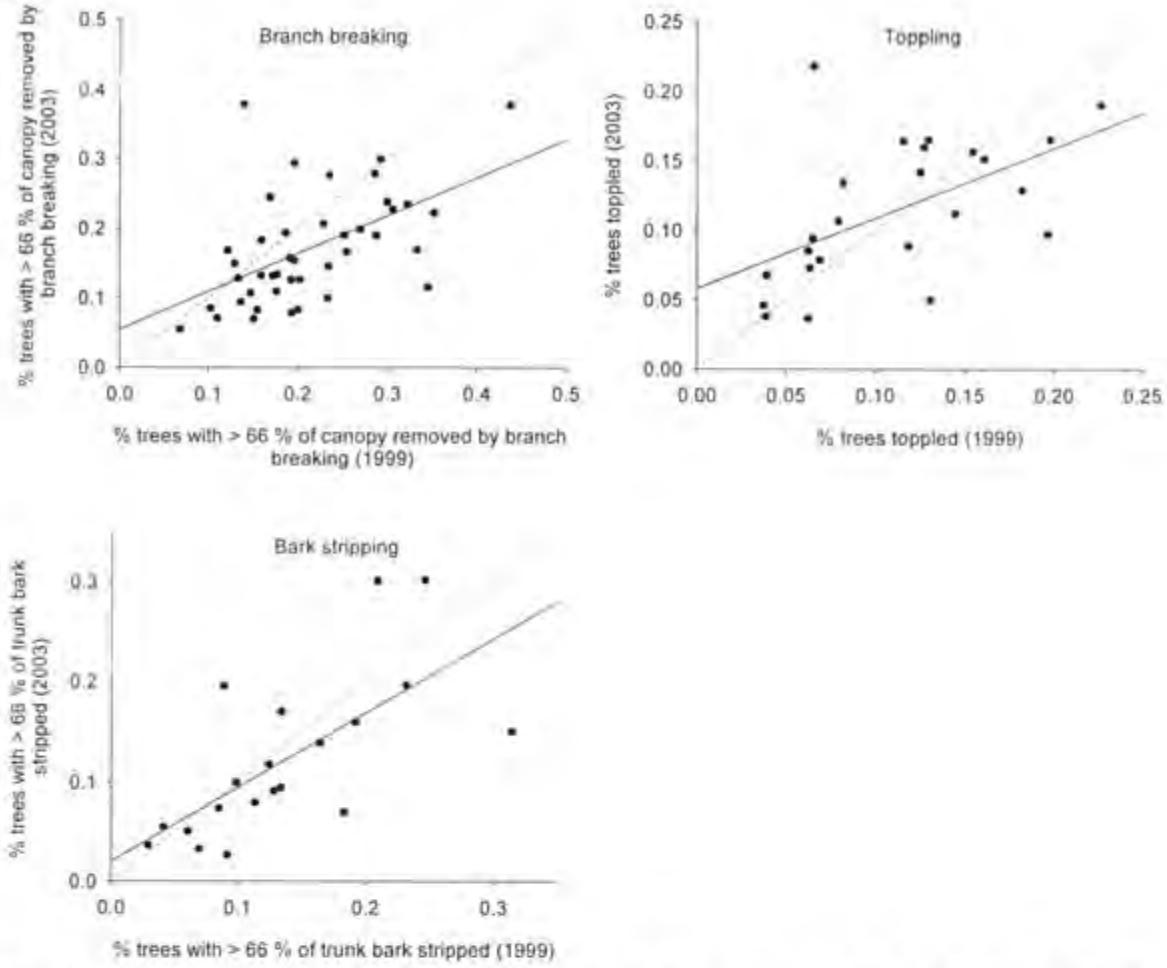

Fig. 3. Species plotted according to the percent of individuals (a) with heavy branch breaking, (b) toppled, and (c) with heavy bark stripping, in 1999 versus 2003. Percentages are arsin√ transformed.

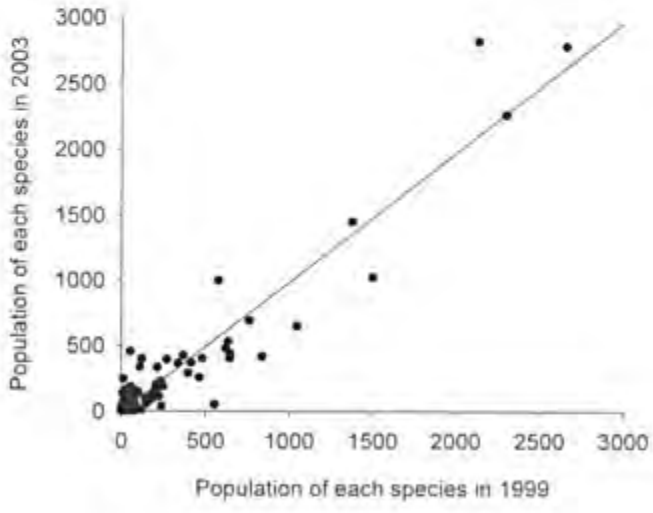

Fig. 4. Species populations in 1999 versus populations in 2003 ($y = .983x$, $r^2 = .909$, $p < .0001$, d.f. = 138).

Utilisation of different sized trees

For all types of use elephants appear to favour larger trees, although this pattern of size class utilisation was less marked for branch breaking (Fig. 5). A comparison of the basal area class, and height class distributions of all the trees in the park for 1999 and 2003, showed the biggest declines occurring in large trees (Fig's 6&7). Trees 6 to 8 m tall showed the largest declines in abundance, but those taller than this showed no decline at all. A comparison of the height class distributions of species favoured by elephants and those avoided by elephants appeared to show a general shift in tree size class distributions to smaller trees from 1999 to 2003 (Fig. 8), whereas avoided species appear to have maintained fairly similar distributions (Fig. 9).

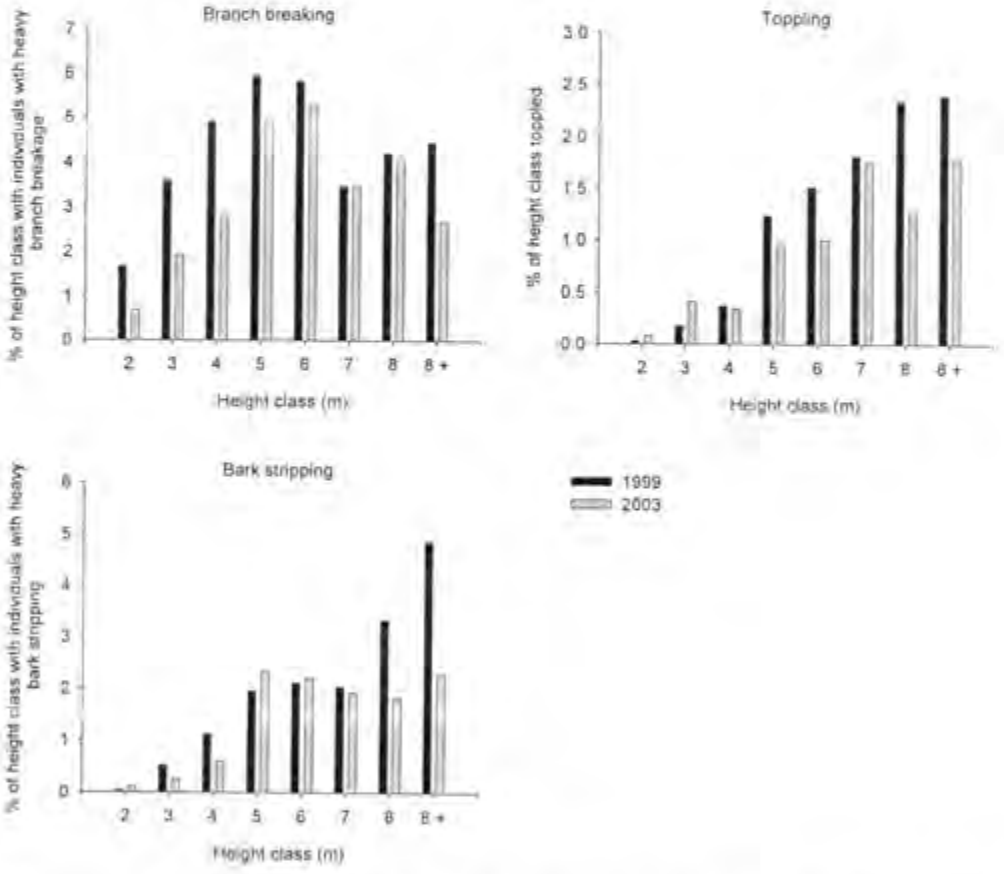

Fig. 5. Percentage of individuals in each height class utilised by elephants for branch breaking, toppling, and bark stripping for both 1999 and 2003. The use of trees in bigger height classes, especially those taller than 4 m, was significant for all types of use (Branch breakage: $X^2 = 2543.6$, Toppling: $X^2 = 143.8$, Bark-stripping: $X^2 = 1358.8$, all $p < .0001$, d.f. = 7)

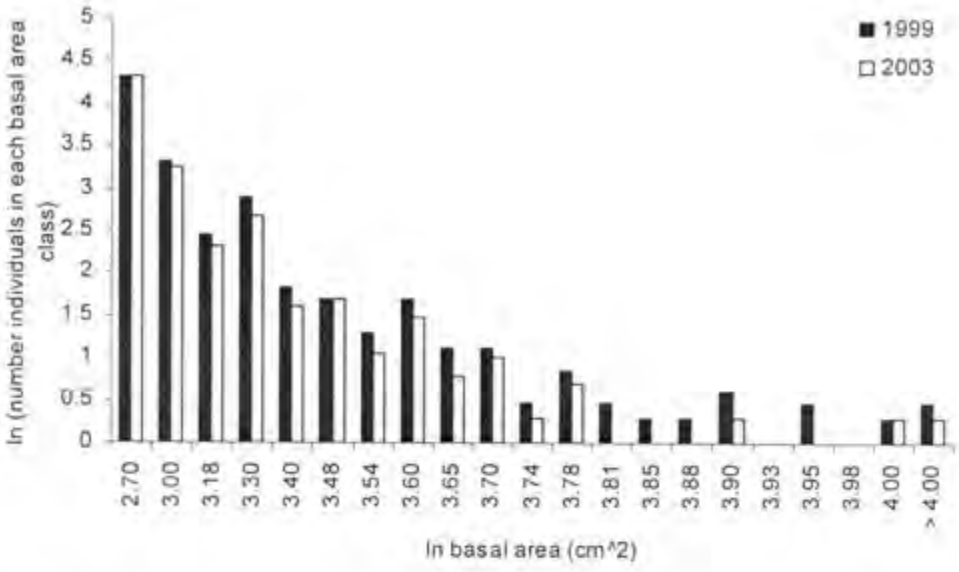

Fig. 6. Basal area (ln transformed) distribution for trees of all species (number in each class ln transformed).

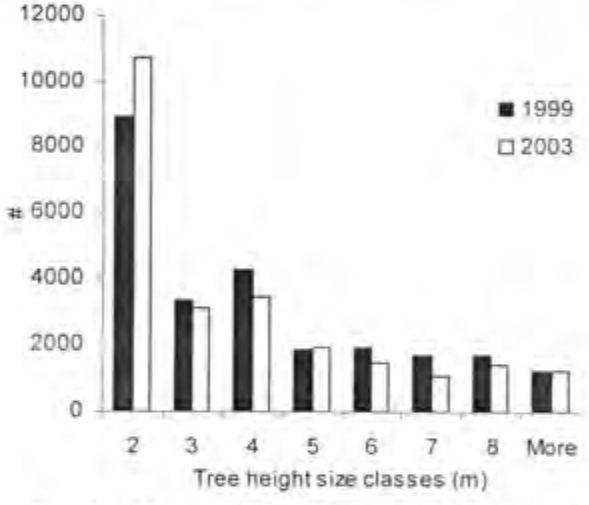

Fig. 7. Height class distribution of trees of all species in 1999 and 2003.

25 173 trees in 1999, 24619 in 2003. t-test shows they are significantly different ($p < 0.00$, $t = 20.73$, $df = 49790$).

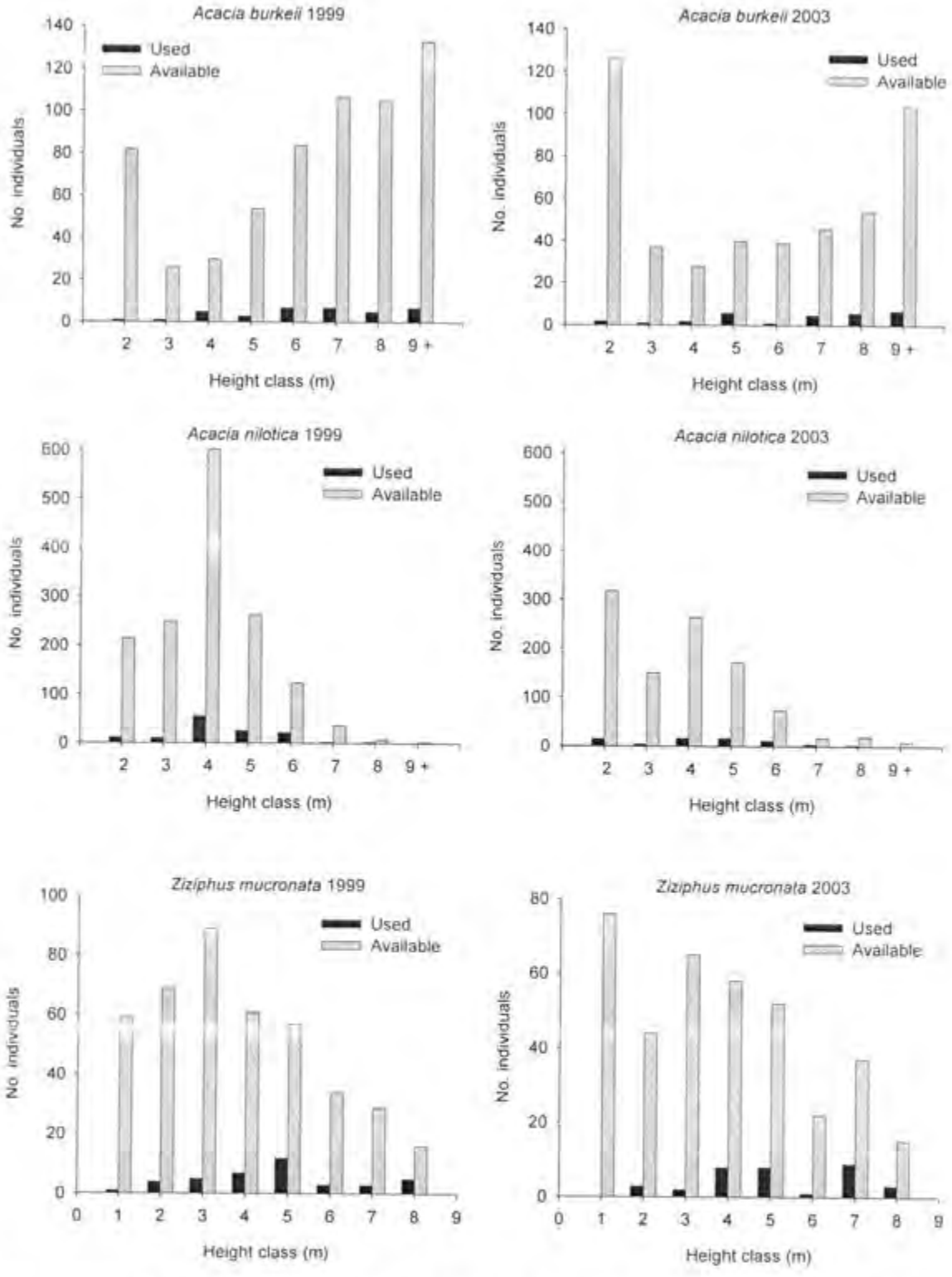

Fig. 8. Actively targeted species' height class distributions for both 1999 and 2003 of number of trees available to elephants in each height class, and the number utilised (all types of utilisation likely to cause tree mortality).

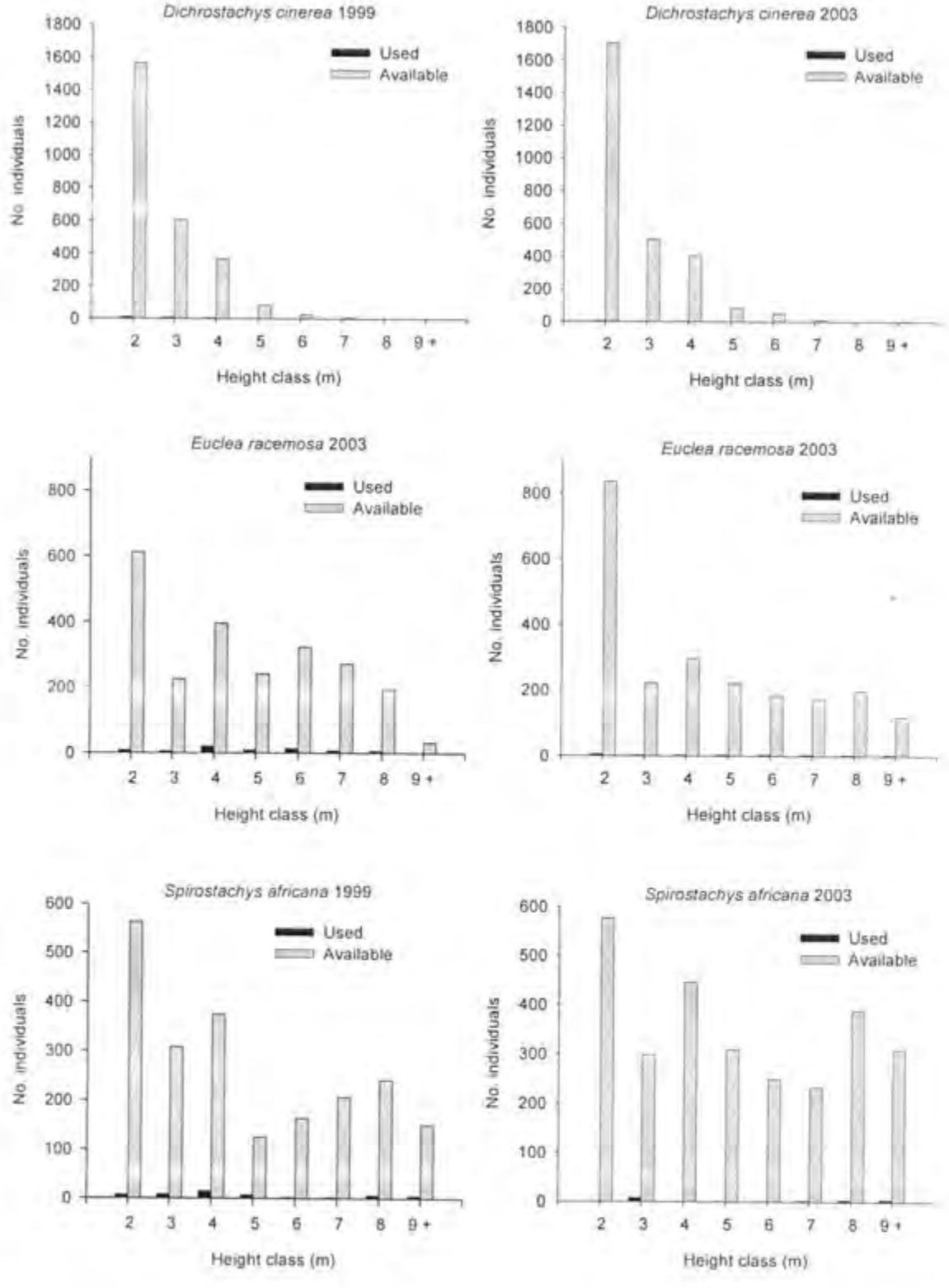

Fig. 9. Under-utilised species' height class distributions for both 1999 and 2003 of number of trees available to elephants in each height class, and the number utilised (all types of utilisation likely to cause tree mortality).

Utilisation of open or closed woodlands

Elephant utilisation was clearly higher in plots with lower densities of trees for all use types (Fig. 10). By and large elephant use appeared to be higher in more open than closed vegetation types, particularly with forests being distinctly avoided. The pattern, however, in woodlands is less clear and varies depending on the dominant vegetation type (Table 3). In general, vegetation types dominated by favoured species of elephants appeared to be more utilised by elephants, whereas those dominated by species avoided by elephants were less utilised. In agreement with the pattern of higher elephant tree use in less dense woodlands, an analysis of whether elephant use was affected by the availability of a species, a plot showed almost all species to be targeted when occurring at low abundances (Table 4).

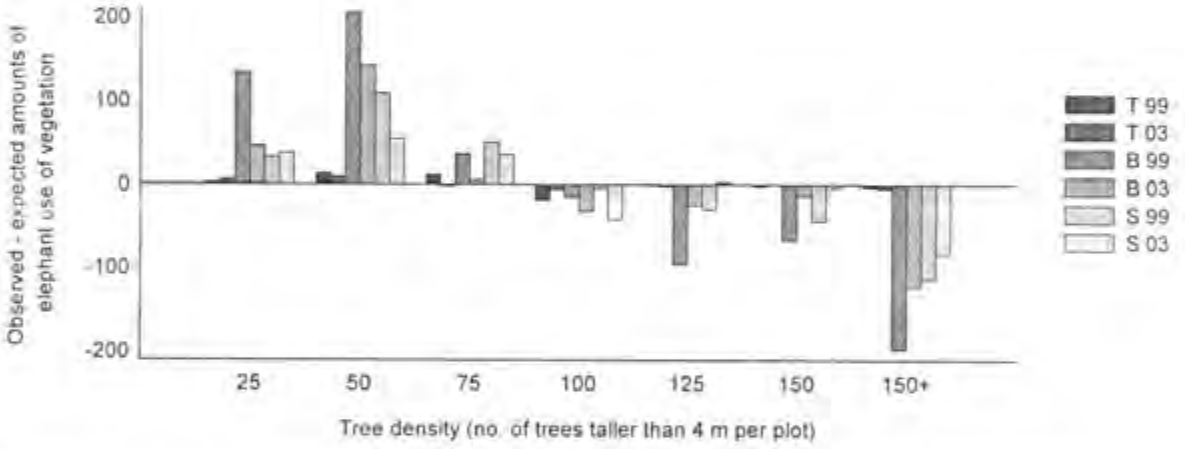

Fig. 10. Observed minus expected numbers of individuals utilised relative to the density of trees > 4 m tall per plot (T = toppling, B = branch breaking, S = bark stripping) for both 1999 and 2003 (X^2 = 21, 22, 197, 84, 107 and 92 for T99, T03, B99, B03, S99 and S03 respectively, all $p < .01$, d.f. = 6).

Table 3. Observed minus expected numbers of individuals utilised, relative to the proportion of plots of a particular vegetation type to the total number of plots in the park. Results for all use types and for both years (except toppling in 1999 as too many vegetation types had expected values below five). Dominant species of each vegetation type listed in brackets.

Vegetation type	Observed - expected no's of trees with damage				
	B 1999	B 2003	T 1999	S 1999	S 2003
Grasslands	-	4	-	-	5
Invaded grasslands	-	64	-	-	30
O. Woodland (*Acacia nigrescens*)	6	**-60**	**-6**	**-33**	**-34**
O. Woodland (*Acacia tortilis*)	-5	25	-4	-14	1
Thicket (*Acacia davyi*)	4	-23	0	-1	-17
Woodland	-	35	-		1
Woodland (*Acacia burkeii*)	**132**	**23**	**29**	**21**	0
Woodland (*Acacia gerardii, Spirostachys africana*)	-5	-28	-9	77	39
Woodland (*Acacia karoo*)	-17	9	-1	0	6
Woodland (*Acacia nilotica*)	**91**	**19**	-5	**91**	**31**
Woodland (*Combretum molle, Combretum apiculatum*)	6	-41	2	-19	-26
Woodland (*Ochna arborea, Spirostachys africana*)	-30	75	-2	-19	17
Woodland (*Spirostachys africana*)	**-15**	**-63**	**-7**	**-12**	**-8**
C. Woodland (*Acacia burkeii, Antidesma venosum*)	33	-	0	14	-
C. Woodland (*Acacia nilotica, Acacia gerardii*)	55	13	-5	15	-7
C. Woodland (*Euclea divinorum*)	-60	16	3	-73	-13
Riv. Forest (*Spirostachys africana*)	33	**-9**	**-6**	**-29**	**-14**
Riv.Forest (*Acacia robusta, Ficus sycomorus*)	**35**	**67**	**13**	**99**	**47**
Forest	**-263**	**-38**	**-2**	**-117**	**-31**
X^2	253	25	106	120	150
p-value	p < .000	p < .087	p < .000	p < 000	p < 000
df	15	17	15	17	17

Table 4. Summary of frequency dependence power functions for different types of utilisation and for different years. The power function is fitted to the % of a species available versus the % use of that particular species for all plots the species was present in. Power function is of the form $y = Ax^B$. 'A' gives an indication of elephant preference for the species. 'B' describes the frequency dependence of utilisation (B<1: sp. targeted at low densities; B=1: sp. utilisation frequency independent; B>1: sp. targeted at high densities). r^2 of power function fit to data, and number of plots used for regression given.

Species	A	B	r^2	# plots
Branch breaking 1999				
Acacia grandicornuta	2.58	0.72	0.79	14
Acacia nilotica	2.68	0.7	0.72	49
Acacia robusta	2.48	0.73	0.83	31
Euclea racemosa	2.46	0.6	0.53	54
Rhus pentheri	2.74	0.75	0.74	40
Spirostachys africana	1.28	0.9	0.74	45
Branch breaking 2003				
Acacia gerardii	3.18	0.69	0.58	35
Acacia grandicornuta	1.87	0.78	0.91	14
Acacia karoo	3.48	0.67	0.74	40
Acacia nilotica	2.62	0.77	0.64	54
Acacia robusta	3.02	0.68	0.55	29
Acacia tortilis	3.82	0.66	0.83	18
Euclea racemosa	1.37	0.85	0.65	44
Rhus pentheri	2.34	0.83	0.7	36
Spirostachys africana	1.77	0.73	0.57	42
Ziziphus mucronata	3.52	0.68	0.53	62
Toppling 1999				
Acacia nilotica	26.72	0.3	0.41	13
Berchemia zeyheri	41.52	0.28	0.24	11
Ziziphus mucronata	32.79	0.34	0.21	11
Toppling 2003				
Berchemia zeyheri	62.34	-0.01	0.0014	11
Ziziphus mucronata	62.34	-0.01	0.0014	8
Bark stripping 1999				
Acacia burkei	23.73	0.11	0.01	18
Acacia nigrescens	6.29	0.59	0.63	9
Acacia nilotica	7.75	0.54	0.48	42
Acacia robusta	8.16	0.5	0.64	30
Dichrostachys cinerea	9.36	0.19	0.1	15
Euclea racemosa	2.5	0.55	0.28	18
Schotia brachypetala	8.61	0.46	0.25	32
Spirostachys africana	1.65	0.83	0.47	18
Bark stripping 2003				
Acacia gerardii	9.22	0.47	0.29	19
Acacia grandicornuta	11.48	0.47	0.56	18
Acacia nilotica	12.02	0.42	0.46	52
Acacia robusta	11.47	0.38	0.19	24
Schotia brachypetala	10.69	0.56	0.34	30
Spirostachys africana	2.06	0.72	0.25	25

Discussion

Massive changes in vegetation composition and structure occurred across the globe at the end of the Pleistocene (Lambert & Holling 1998). The role, however, that the extinction of most of the world's megafauna had in these changes is highly contentious (Lambert & Holling 1998, Miller *et al.* 2005, Johnson 2005). The keystone megaherbivore hypothesis contends that the extinction of the megafauna led to a change from "parklike woodlands and mosaic grasslands" to "the more uniform forests and prairie grasslands we find today" (Owen-Smith 1987). In 1987 Owen-Smith suggested that the Hluhluwe-iMfolozi Park could serve as an "experimental test of the keystone herbivore hypothesis", but stated that, "it is likely to be decades before the outcome is clear". Almost twenty years on from this statement, we have evidence that is contradictory to some of the predictions of this hypothesis, and in particular question the role of megaherbivores in opening up woodlands and forests.

One of the predictions of the keystone megaherbivore hypothesis is that megaherbivore disturbance should lead to an increase in faster-growing species, which should have less chemical defences (Owen-Smith 1987). In this study elephants were shown to selectively target certain species, such as *Acacia* species, *Berchemia zeyheri* and *Ziziphus mucronata*, but avoid certain species, particularly *Acacia karoo, Dicrostachys cinerea, Euclea racemosa* and *Spirostachys africana*. Similar species preferences have been shown in other studies (Guy 1976, Wiseman *et al.* 2004). The impact on preferred species appears to have increased, but has decreased for avoided species, from 1999 to 2003. The decline in population sizes of preferred species, and increase of avoided species, thus, seems to be directly attributable to elephant usage of these species. However, the species which elephants appear to be encouraging are not all highly palatable species as the keystone megaherbivore hypothesis predicts. For instance, *Spirostachys africana*, the Tambothi, is well known for its poisonous properties. *Acacia karoo* and *Dichrostachys cinerea* are both highly spinescent species, and possibly avoided by herbivores because of this. The largest declines, however, were in the

species, such as *Acacia* spp. and *Ziziphus mucronata*, which are very palatable and favoured by smaller browsers. Elephants were found to favour large trees for all types of utilisation and have likely been the main protagonists of large tree declines in the park. Trees larger than 8 m tall, however, appear to be very little affected by elephant use. This does provide some support for elephants creating "parklike woodlands" which would have had few very large trees and mostly shrubs and grass below in the under-canopy (Owen-Smith 1987). The effect of elephants on vegetation structure, though, appears to depend on whether the species is preferentially targeted or not. Favoured species of elephants showed the greatest changes in size class distributions to smaller size classes. This is also in agreement with the prediction that megaherbivores should reduce vegetation height to be usable by smaller browsers, and increase coppicing through the breaking of branches (Owen-Smith 1987). However, concomitant with these changes in size class distributions of favoured species, was a decline in their population sizes, which would have made the general availability of these species much lower.

Elephants seem unlikely to prevent bush encroachment as they clearly avoid dense woodlands for the utilisation of woody vegetation. Some vegetation types appear to show contradictory patterns to this trend, for instance, riverine forest dominated by *Acacia robusta* and *Ficus sycomorus*, is highly utilised whereas open woodlands dominated by *Acacia nigrescens* appear to be under-utilised. The dominant species of these vegetation types could explain this pattern, as elephants were shown to favour *Acacia robusta* but avoided *Acacia nigrescens* for branch breaking and bark stripping. In light of this evidence, the role of megaherbivores in opening up thickets and creating gaps in forests as suggested by Owen-Smith (1988) seems questionable. Elephants were also found to avoid dense woodlands in Uganda (Beuchner & Dawkins 1961, Wing & Buss 1970) and their effects in forests have largely been to bark-strip trees, and eat understorey herbaceous vegetation and shoots of juvenile trees (Laws 1970, Sheil & Salim 2004). Where elephants do damage forests it appears as if they eliminate forests completely (Laws 1970). The Asian elephant also appears to not

open up forests, causing only crown distortion of trees between 2 - to 5-m tall trees, and is mostly associated with already disturbed and developing vegetation (Mueller-Dombois 1972). Extinct megaherbivore browsers, such as mastodons, possibly then also did not open up woody vegetation.

Our findings do not appear to be in agreement with some of the predictions made by the keystone megaherbivore hypothesis, in particular that faster-growing species with less chemical defences should be favoured, and that closed woodlands would be opened up, by megaherbivore utilisation of vegetation. However, we do find support for megaherbivores reducing overall vegetation height. It is worth noting that in 1987, Owen-Smith attributed declines in many herbivore populations before 1980 in Hluhluwe iMfolozi to the lack of a presence of elephants in the park. A recent report on the trends in herbivore numbers in the park since the 1970's shows that species such as wildebeest, zebra, kudu and waterbuck have all increased in numbers (Balfour 2001). Extrapolations from this, however, are complicated by factors such as drought mortatility in the 1980's and cessation of the culling of most herbivore species after the introduction of elephants.

Support for keystone megaherbivore hypotheses has been provided from evidence from the Siberian tundra. This suggests that megaherbivores promoted the growth of grasslands instead of mosses and shrubs, and speeded up nutrient recycling through their disturbance of the soil and fertilising of the soil (Zimov *et al.* 1995, Zimov 2005). Mud cores from lakes in North America suggest that fires drastically increased after the disappearance of the megafauna, suggesting that fuelwood accumulated in substantial amounts after their demise, thus increasing the frequency of fires. Only about a thousand years later did the species composition of these areas change, as evidenced by a change in pollen, as a result of a changing climate (Kerr 2003). Elephants too are known to cause major changes in vegetation structure and composition, for example, they appear to have been largely responsible for the disappearance of woodlands in Tsavo, Kenya (Leuthold 1996). However, most of these vegetation shifts caused by elephants have been observed at much higher elephant densities

than currently exist in Hluhluwe iMfolozi, which has just over 300 elephants in a 900 km^2 park. Nonetheless, future impact by an increasing elephant population is unlikely to cause an opening up of closed woodlands as suggested by the keystone megaherbivore hypothesis, but seems likely to cause greater loss of trees in open woodlands thus contributing to the creation of uniform grasslands and forests.

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