

A scientific perspective on the management of elephants in the Kruger National Park and elsewhere

N. Owen-Smith^{a*}, G.I.H. Kerley^b, B. Page^c, R. Slotow^c and R.J. van Aarde^d

HOW TO RESPOND TO GROWING ELEPHANT numbers in the Kruger National Park and elsewhere in southern Africa continues to be a contentious issue. In contrast to the public perception, scientists have attained a high degree of consensus on the ecological basis for such decisions. In this article we summarize these ecological principles and the management responses that are indicated, in order to counter some of the misunderstanding that has been evident in the popular media.

Introduction

Standpoints on the management of elephants have tended to be polarized between pro- and anti-culling lobbies, as evidence by articles in a recent issue of *Africa Geographic* magazine (April 2006). Nevertheless, a panel of scientists most knowledgeable about elephants and the consequences of their impacts for ecosystems reached general agreement on their recommendations to the Minister of Environmental Affairs and Tourism at the conclusion of the recent (18 January 2006) 'Elephant Science Roundtable' that he convened for this purpose. To quote from the consensus statement released:

1. There is no compelling evidence for the need for immediate, large-scale reduction of elephant numbers in the Kruger National Park (KNP).
2. Nevertheless, in some protected areas including the KNP elephant density, distribution and population structure may need to be managed locally to meet biodiversity and other objectives.

The first recommendation might seem surprising to those who contend that the need to reduce elephant numbers, and

hence their impacts, is obvious. To those who challenge the need for any action that might entail the killing of elephants, the acknowledgement by the panel that management intervention could be justified in some situations, not only in smaller reserves but even perhaps in parts of the KNP, could be disturbing. These recommendations may therefore be interpreted as contentious from both sides of the debate.

In this article, we (1) outline the background context leading up to the Elephant Science Roundtable, (2) explain some of the ecological principles relevant to elephant management, (3) suggest the adaptive management responses needed in the face of uncertainty, and (4) acknowledge some of the wider concerns outside science. In conclusion, we summarize the recommendations arising from our perspective as scientists deeply involved in addressing some of these ecological issues in our own research.

Background

The Elephant Science Roundtable followed a series of consultative fora around elephant management issues. The review process has been unusually comprehensive, and has attracted widespread international and local interest. It is thus important to place the scientific assessment within the framework of this wider public review and the actions that led to it. Some of the earlier background has been outlined elsewhere.¹

A policy of culling to maintain the elephant population below a ceiling of around 7000 animals was first implemented in the KNP in 1967, following concern about the effects that these animals were having on vegetation.² A total of 16 027 animals was removed between 1967 and 1994.³ In 1994, animal rights groups challenged the culling policy as lacking a scientific foundation, which led to a moratorium being placed on further killing, while the policy underwent review (although live removals continued). Following an initial public debate, a work-

shop held in 1996 brought together local and international conservationists to review the policy. The outcome was a management plan that involved the zonation of the KNP into two 'high elephant impact' zones, within which culling would be suspended, two 'low elephant impact' zones, within which elephant numbers would be progressively reduced to some lower density, and two 'botanical reserves' where elephant presence would be allowed but at some controlled level.^{4,5}

This policy was not implemented, however, for various reasons and the review process was re-opened in late 2004 with a 'Great Elephant Debate' organized by the Wildlife and Environment Society of South Africa. This was followed by a 'Great Elephant Indaba' organized by South African National Parks (SANParks).⁶ Divergent public views on the culling issue were presented at both of these open meetings and, following this, current scientific knowledge and understanding concerning elephants and their impacts was synthesized at the Luiperdskloof 'Elephant Science' workshop.⁷ From this base, scientific and management staff of SANParks recommended, through their director and board of control to the minister, that culling be recognized as a legitimate option for the management of elephants, subject to defined norms and standards.⁸ Meanwhile, the 'Elephants Alive Initiative' (a consortium of animal rights groups, scientists, conservationists and legal experts) convened a workshop in mid-2005 to challenge the anticipated resumption of culling in the KNP. Later that year, the minister met with some of the groups opposed to culling, together with leading conservation NGOs. Representatives of these NGOs supported the urgent need for elephant populations to be controlled so as to avoid threatened losses of endemic and indigenous species.⁹ However, scientists present recommended that further consultation should take place with experts most knowledgeable about elephants.

The minister accordingly assembled a panel of 10 scientists actively engaged in elephant-related research to provide answers to these simple questions: 1) Are there too many elephants? 2) Are elephants causing irreversible damage to biodiversity? 3) Is action needed to reduce elephant densities? Answers were requested for both the KNP and elsewhere in South Africa. The ultimate purpose was to inform the minister and thereby provide him with an objective basis for the norms and standards needed to guide elephant management throughout South Africa.⁸ At the time of writing, the final policy definition is still pending.

^aCentre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa.

^bCentre for African Conservation Ecology, Department of Zoology, P.O. Box 77000, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa.

^cAmarula Elephant Research Programme, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Howard College Campus, Durban 4041, South Africa.

^dConservation Ecology Research Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

*Author for correspondence.
E-mail: norman@gecko.biol.wits.ac.za

Underlying ecological principles and guidelines

Below we outline some of the ecological considerations that led to the panel's recommendations, and suggest some guidelines for the management actions that are needed in this light.

The formerly capped population of around 7000 elephants in the Kruger National Park should not be construed as an ecological carrying capacity

Claims have been made that the elephant population in the KNP, now approaching 13 000, has exceeded some previously recognized 'carrying capacity' of 7000 animals. Pienaar *et al.*² recognized that 'theoretically a carrying capacity of 1–4 elephants per square mile, depending on the existing vegetation, available water supplies and size of the area, holds for the majority of elephant habitats in Africa', implying a potential total of 20 000 or more elephants within the 19 485 km² extent of the KNP. However, in the light of a vegetation survey, van Wyk and Fairall¹⁰ decided that 'the highest number of elephants which could be carried ... would be 0.75/mile² (i.e. 6000 elephants) if the total destruction of the vulnerable areas near water is not to result.' Based on this recommendation, and dispersal movements by elephants noted around that time, the National Parks Board approved the recommendation for culling, stating that 'Until the water provision programme has been finalized in its entirety, both elephant and buffalo populations of the KNP should be held at their current level....'³ However, the concern about vegetation damage was raised at a time in the early 1960s, when rainfall had remained well below average for five successive years. Hence the institution of the population ceiling was a precautionary reaction to the combined impacts of elephants and drought conditions on the state of the vegetation. In SANPark's terminology, it reflects a 'threshold of potential concern' (TPC). It represents neither the carrying capacity recognized by ecologists, nor its usage by resource managers aiming at a sustainable yield.^{11,12}

Nevertheless, there are three senses in which the carrying capacity concept is commonly used:

- *Ecological* carrying capacity is the population level at which the net population growth rate becomes zero, or more generally the average density maintained over some extended period.¹¹ For a growing population to become stable, appropriate changes must take place in the birth rate, death rate, rate of dispersal, or some combination thereof. Most generally, such demographic changes are

the result of intensified competition for scarce food resources. In such circumstances, large herbivores inevitably have some impact on the structure and composition of the vegetation. The consequences of these changes in vegetation, and the extent to which they might be reversible or persistent, raises other issues.

- *Economic* carrying capacity is the reduced stocking density maintained by live-stock farmers to maximize the yield of meat or other products.¹¹ At this density, the population attains its maximum incremental growth, and hence produces the greatest surplus for harvesting. With lower animal numbers, vegetation resources appear less degraded, although not necessarily more productive than at ecological carrying capacity.
- *Aesthetic* carrying capacity is the population level maintained to prevent some undesirable change in the environment. Most superficially, this may be done to avoid alteration of the vegetation from some benchmark state.¹³ This position is untenable, as vegetation structure and composition inevitably change over time,^{14,15} as we discuss below. Nevertheless, certain vegetation features may be highly valued assets, such as the big trees [for example, marula (*Sclerocarya caffra*), baobab (*Adansonia digitata*), knobthorn (*Acacia nigrescens*)] which are characteristic of the lowveld region within which the KNP is situated. Furthermore, some of these trees and the animals they support may be important functional components of the biodiversity of the region. A healthy vegetation cover also provides valuable ecosystem services in terms of protecting soils from erosion and promoting water infiltration.

What is aesthetically desirable can be challenged, even with regard to supposedly objective biodiversity objectives, for instance, the retention of rare but functionally minor species. This falls outside the scientific realm and raises societal objectives in setting aside land for protected areas. Conflicts among different aesthetics or ethics can arise. Achieving the goals set by society, such as retaining the biodiversity of the lowveld region of South Africa 'in all its facets and fluxes', provides the framework for the strategic adaptive management policy adopted for the KNP.¹⁶

An important concern is whether the changes that are deemed undesirable are irreversible. Here a time frame for 'irreversibility' needs to be defined — from a human perspective, we cannot look much beyond the responsibilities of one generation to the next, that is, further ahead than

about 25 years. However, ecosystem processes, particularly those involved in woodland dynamics, extend well beyond this time frame. Savanna ecosystems seem especially resilient in recovering from perturbations.¹⁷ Nevertheless, some areas may be transformed into less desirable shrub thicket or treeless grassland states for several decades. Whether such changes have adverse ecological consequences depends mainly on their extent, as we discuss below.

In Kruger, big trees have declined despite past capping of elephant numbers

Many large trees have been lost from sections of the KNP and in some areas big trees have been replaced by a denser shrub cover.¹⁸ However, these changes occurred through the period when the elephant population in the park was held around 7000; thus, assuming elephants to be responsible, a far lower elephant population would be needed to halt such loss. The problem is not the inevitable mortality among big trees, but rather the lack of recruitment from smaller size classes to replace them. Other agents such as fire^{19,20} and browsing, for instance by impala (*Aepyceros melampus*),²¹ clearly also play a role in tree establishment and growth. Rainfall patterns may also have changed from the time, several centuries back, when the big trees that we now see were established. Regionally, low elephant numbers, due to over-hunting at that time, probably also favoured the establishment of these woodlands as it apparently did elsewhere.²²

There is no benchmark against which to judge an ideal vegetation state for Kruger

Large herbivores introduced into an environment from which they have been absent usually change the vegetation in some way.²³ When areas that later became part of the KNP were first given protected status in 1898, no more than 10–20 elephants remained, and reports indicate few elephants in the region earlier in the 19th century.² Since there is clearly nothing unsuitable about the habitats to support elephants, this seems to be an indication of how effectively the ivory trade had eliminated elephants across large parts of Africa. Hence the vegetation recorded historically in the KNP assumed its form in the absence of elephants, together with low densities of other large herbivores. The state of the vegetation must inevitably be changed following increases in the abundance of elephants and other species. Establishment during episodic windows of opportunity seems to be a general feature of woodlands subject to wide

variability in rainfall, fire frequency and herbivory.^{24–26}

Claims of ecological disasters from elsewhere have been greatly exaggerated

The case studies invoked to indicate the adverse consequences of elephant overpopulation include Tsavo East National Park in Kenya, Chobe National Park in Botswana, and Hwange National Park in Zimbabwe. While certain sections of these protected areas appear intensely disturbed, the vast part seems ecologically intact (N. Owen-Smith, personal observations). Research conducted in these parks has not revealed substantial consequences for either animal or plant diversity, despite elephant populations of 1–2 animals per km² regionally and local concentrations of 4–8 elephants per km² (refs 26–28). Changes in species composition responding to altered habitat, for example, the decline in browsers in Tsavo, was counterbalanced by an increase in grazers.²⁹ Riparian woodlands have regenerated in Tsavo following the die-off of many elephants and poaching, indicating that the changes wrought by elephants were not irreversible even in this sensitive arid environment.²⁷ Nevertheless, baobab trees have become scarce within Tsavo East and South Luangwa parks, while remaining abundant outside park boundaries (N. Owen-Smith, personal observations).

Elephants were identified as mainly responsible for the near-extinction of *Acacia xanthophloea* woodland in Amboseli Park in Kenya, through preventing regeneration.³⁰ The mosaic of wooded and open habitats across this region appears to have been the outcome of a spatial interaction between elephants and Maasai pastoralists in past times. A trend towards grassland at the expense of woody vegetation threatens the loss of animal species dependent on large trees as habitat.³¹

The concept of a balance of nature is outmoded

It is popularly believed that protected areas would persist in some pristine state if left alone by humans. However, there has been growing recognition among ecologists that flux is an integral part of ecosystem dynamics, and that temporal and spatial variability is important in maintaining a diversity of plants and animals.^{32,33} Disturbances such as fire, floods and droughts can help generate space for a variety of species to coexist, and from this perspective the disturbing effects of elephants on vegetation could likewise be beneficial.

Nevertheless, if disturbances are too severe or frequent, adverse changes could result.³⁴ Furthermore, changes which

might have been benign in the past could well proceed to extremes when animal movements are constrained by boundary fences and modified by the provision of artificial waterpoints.^{35–37} The possible impact of hunting by humans, starting well before the arrival of firearms, on elephant abundance is contentious. We believe that the most important influence of human hunters and pastoralists was on the spatial distribution of elephants, reducing their impacts locally rather than having much effect on their overall numbers.

We suggest that it is not the local severity of the disturbance to vegetation induced by elephants that is important, but rather the spatial extent of such influences. Local overgrazing or overbrowsing by various large herbivores is widely observed, and is inconsequential or even beneficial if only a small portion of the area is affected.³⁸ Concern about adverse consequence rises when such changes spread to cover a large fraction of the available area, thereby reducing the mosaic diversity of habitats. However, severe impacts have remained localized even in places such as Chobe National Park, despite the huge elephant population.²⁶

Establishing a heterogeneous spatial template is more effective than continually counteracting change

Spatial variability in the distribution of elephants enables some areas to escape severe impacts, as noted above. However, the heterogeneity that formerly prevailed becomes restricted in fenced, protected areas with ecologically arbitrary boundaries. Whereas, in unfenced parks, elephants generally move between distinct wet and dry season ranges, in Kruger the seasonal ranges of breeding groups largely overlap (R. J. van Aarde, unpublished observations).

Fencing off parts of the area to preclude elephant impacts has been done in the Addo Elephant National Park, Tembe Elephant Park and Phinda Resource Reserve. Such extreme intervention is only practical for relatively small areas, and considerable effort is needed to maintain fences. A more effective measure for the KNP would be to restrict the spatial distribution of surface water during the dry season period when elephants need to drink every day or two. The threat to biodiversity comes not from the numbers of elephants, but from their effect on particular components of the vegetation at certain times of the year. For most of the wet season elephants consume largely grass. Impacts on trees and, in particular, felling and debarking of large trees, tend to be concentrated during the latter part

of the dry season when the dry grass is less nutritious than woody plant parts. This is heightened in dry years when food becomes sparse.^{39,40} Trees remote from water will escape such impacts at this time of the year. The past policy of augmenting the natural surface water in rivers and springs through building dams and sinking boreholes spreads the effects of elephants over a wider portion of the landscape at this critical time of the year.⁴¹ Permanently supplying surface water away from rivers does not allow adequate time for plant regeneration, which occurs normally when the natural pools retaining water through the dry season depend on local rainfall. Trees growing in riparian zones may be relatively more resistant to elephant impacts through being deep-rooted and adapted to recover from major disturbances such as floods. The species that seem to be most vulnerable to depression from elephant damage, such as baobabs and marulas, tend to grow mainly in upland regions away from water. Furthermore, the distribution of elephant bulls, which have a relatively much greater effect on trees than the breeding herd segment,^{42,43} needs most attention.

Density feedbacks must ultimately curtail the growth of elephant populations

Density influences on population growth are inevitable through the effects of accentuated competition for available resources, depletion of the best quality food types and the costs of travelling further to find suitable food or colonizing marginal lands.⁴⁴ Uncertainty is confined to the stage at which such density regulation will become effective, recognizing that the density level itself will be a function of rainfall as well as habitat conditions.⁴⁶ Very large mammals such as elephants seem to maintain a population growth rate near their maximum until quite close to the ceiling set by food resources.⁴⁷ The Addo elephant population shows no evidence of any density feedback on population growth, despite an abundance level approaching 4 elephants per km², a demonstrated decline in forage availability and loss of some plant species.⁴⁸ However, this park's capacity to support elephants may be exceptionally high, due to year-round rainfall, the prevalence of nutritious evergreen thicket, and artificial waterpoints. In contrast, the Hwange population appears to be stabilizing at a total of between 30 000 and 40 000 elephants, that is, 2–3 per km² (S. Chamaille-Jammes *et al.*, unpublished manuscript), with local water supplies contributing to the variability. Density feedbacks have been documented among elephant populations

elsewhere,⁴⁹⁻⁵¹ as well as among other megaherbivore species.⁵²

A demographic model indicates that reducing the continuing growth of Kruger's elephant population to zero could be brought about through a change of about 60% in specific vital rates — lengthening of the interval between calves from 3.8 to 6 years, delay in the age at first parturition from 11 to 18 years, and reduction in calf survival between birth and 5 years (the age at weaning) from 91% to 55% — without any change in age-specific survival among adults (N. Owen-Smith, unpublished observations). Elephant population growth seems particularly sensitive to changes in inter-calving intervals.^{50,53} Adjustments in these vital rates will not be instantaneous, however, and there could be a lag of up to a generation before population growth is halted because of continuing recruitment into the breeding segment of young animals already born. Periodic mortality among both young and adult animals during droughts, as documented in Hwange,^{54,55} would reduce the extent of the reproductive changes needed to produce population stasis. The disastrous mortality in Tsavo East, when around 7000 elephants died during extreme drought conditions following compression of elephants into the park,⁵⁶ has not been repeated elsewhere. Nevertheless, lags in the response of elephants to changing vegetation and hence food availability could theoretically generate oscillations in the abundance of both elephants and woodlands, rather than any persistent equilibrium.⁵⁷

Restrictions in surface water distribution could enhance density effects by crowding the elephant population into a more limited region of the landscape at the time of the year when resource limitations are most effective. Travelling back and forth between riparian areas, depleted of adequate quality food, and feeding areas further inland, could place an additional stress on young calves, thereby reducing their chances of survival to adulthood. Water restrictions may also be particularly important under drought conditions, when high mortality among young elephants has been documented.⁵⁵ Crowding also attracts the attention of predators such as lions, which have been killing elephants concentrating near water in northern Botswana (D. Joubert, unpublished manuscript; B. Page, unpublished observations).

Active adaptive management in the face of uncertainty

Applying the precautionary principle

Scientific uncertainties remain because the longer-term consequences of high

elephant densities have not yet been observed. Reducing artificial waterpoints will contribute towards restricting the dry season distribution of elephants, but how effective this will be is debatable because perennial rivers and pools in seasonal streams still offer fairly widespread drinking water. Delays of uncertain duration will occur in the demographic responses of elephants to changing local densities. For savanna tree populations, successful recruitment may occur only at decadal or longer intervals, and is subject to various influences — seasonal rainfall patterns, frequency of fires, and predation on seeds by small mammals and insects as well as browsing of seedlings by ungulates.⁵⁸

The precautionary principle invoked to deal with uncertainty could be applied in two contrasting ways. One option is to keep elephant numbers generally low in the hope of preventing feared losses in biodiversity components. The other option is to avoid killing elephants until it has been clearly established that a larger population would indeed lead to losses in biodiversity before stabilizing at some resource-limited level. Obviously, these two perspectives relate to the standpoints taken by pro- versus anti-culling lobbies.

A more perceptive approach would be to manage differentially so as to establish the consequences, and in particular to allow changes to progress towards extremes in selected places to ascertain just where the thresholds beyond which no recovery takes place lie. The previously defined, but not applied, policy of establishing designated zones of high and low impact was a move in this direction.

Targeting the problem

Blanket culling of elephants to contain population increase is a crude response to a problem that is not simply one of elephant numbers, but rather of the spatial and temporal distribution of the impacts of a segment of the population within specific landscapes. It is costly, enduring and distracting for managers. Interventions need not entail killing many elephants.⁵³ Restricting the availability of surface water in sensitive regions has already been suggested above. Localized harassment, which may require killing some animals, could be focused particularly on the bulls, which are responsible for a disproportionate share of the most severe impacts on trees.^{42,43}

For the KNP, progress towards identifying specific sources of worry has already been made through the specification of 'thresholds of potential concern' (TPCs) by its scientists in consultation with outside experts.¹³ These thresholds need to be made spatially explicit. For example, the

elimination of big trees may be tolerated in some regions as long as other areas remain where these assets persist. Limitations in spatial heterogeneity even within large protected areas like the KNP could be alleviated through expansion of the area available for elephant movements by developments such as the Greater Limpopo Transfrontier Park, which may ultimately stretch over more than 36 000 km².⁵⁹

Manipulating only one component of an ecosystem is likely to be ineffective

Ecosystems incorporate complex linkages between many animal and plant species. Reductions in elephant abundance alone would lead to compensatory responses by other populations, with unforeseen ramifications on biodiversity. An example is the water provision programme in the KNP, designed to protect less common ungulate species from undesirable declines during droughts. Instead, this programme promoted the spread of common water-dependent grazers and their associated predators.⁶⁰ It also enabled elephants to occupy most of the KNP throughout the year. Such perpetual tinkering to meet aesthetic objectives seems impractical. Manipulating elephant numbers also provides no insurance that changes induced by them will be restored, since many other species may keep a system that has been altered by elephants in the transformed state.⁶¹

Different measures may be needed for small reserves

In state and private protected areas covering less than 1000 km², the space available to elephants falls below the typical home range size, restricting or preventing wider movements. Hence, all sections become vulnerable to elephant impacts throughout the year. Biochemical contraception has been proposed as a humane way to halt or slow population growth, and may be practical for populations numbering a few hundred or less.⁶² Population increase could also be restricted by distorting the sex ratio towards an extreme lack of either males or females, thereby curtailing reproductive output. In many of these areas, the presence of elephants may be incompatible with the primary aim of conserving a specific vegetation type (such as sand forest in Tembe Elephant Park^{63,64}). Sections preserving endemic plant species may need to be fenced to prevent access by elephants, as has been done in the Addo Elephant Park.⁶⁵ Culling, if essential, would need to be done sensitively so as not to conflict with ecotourism objectives, which are the primary aim of most private reserves. Small reserves also provide opportunities

for experimentation allowing the consequences of different densities of elephants in particular vegetation types to be documented, in particular the impact of much higher levels than those projected for the KNP in the near future.

How much larger than 1000 km² must an area be before little intervention is needed? Is the KNP, spanning almost 20 000 km², big enough to be left alone? The answer depends not only on the size of the area, but also on the distribution of food and water resources governing where the main effects of elephants on vegetation occur.¹⁴¹ With surface water within the daily travelling range of elephants across virtually the entire park area, even during droughts,⁶⁶ the KNP may not be large enough to provide spatial refuges for woodland regeneration. How far the closure of many artificial water points currently in progress will achieve this end remains uncertain, although it will certainly help. Some elephants may still need to be removed from some places where sensitive species or habitats occur.

Supporting research is needed

TPCs assume that there are thresholds of change beyond which undesirable and irreversible situations might develop. They are hypothetical, and thus need to be tested by exploring the actual outcomes. If differential management seems unlikely to deliver an answer within a reasonably immediate time frame, experimental manipulations may be needed to establish whether the consequences of persistently high elephant densities are as deleterious as expected in specific landscapes. Where experimentation is impractical, models are needed to project the likely consequences with a high degree of confidence. Predicting the effects of elephants, other browsers, fire and climatic variability on vegetation dynamics and habitat conditions for other species requires reliable specification of how these factors interact within specific ecosystem contexts.

At this stage, we know little about processes governing the regeneration of savanna woodlands, except that many factors besides elephants potentially influence recruitment into the tall tree stage, with various contingencies involved. Home ranges of elephants have been mapped in Kruger,⁶⁷ but what governs movements within these home ranges at different times of the year, and hence local vegetation impacts, and excursions beyond home range boundaries into new areas, remains unknown. Specific studies to reduce current uncertainty concerning these processes in particular are crucial.

Wider considerations

The ultimate objectives of natural

resource management are decided by society at large through democratic processes, including scientists as interested and concerned members of the public. In South Africa, the management of national parks is currently structured under a biodiversity mandate passed on to it through the institutional responsibility conferred by central government.⁸ Society must ultimately judge the balance between local disappearance of some rare plants or the loss of a more substantial component of ecosystem diversity, and the lives of the elephants killed to prevent this loss. This raises ethical and aesthetic considerations. A philosophical assessment of the ethical issues concluded, '...if culling is to be used, it must only be used as a last resort once reasonable people judge that all possible other options have been explored and exhausted' (H. Lotter, unpublished manuscript). Scientists recognize that change is an integral feature of natural ecosystems which contributes importantly towards the maintenance of biodiversity. The wider public may be less tolerant of such changes, because these threaten other aesthetic or material objectives. Focusing management interventions on elephants alone may be ineffective if additional factors are involved in species losses, in particular the effects of climate change on species distribution patterns. The role of research in decision-making is, specifically, 'to identify the class of technically sound options, and to provide information on how to achieve the chosen option.'⁴⁵ We emphasize that management decisions must reconcile scientific principles with economic, political, social and aesthetic considerations in order to achieve their mandated aims.

Conclusions

In conclusion, we reiterate the following points highlighted in this review:

1. The previously maintained ceiling of around 7000 elephants in the KNP should not be construed as a carrying capacity.
2. Manipulating elephant numbers alone may have ramifying consequences.
3. Big trees have declined in the KNP despite past capping of elephant numbers.
4. There is no benchmark against which to judge an ideal vegetation state for the KNP.
5. Claimed disaster scenarios from elsewhere have been greatly exaggerated.
6. Plant species losses have been documented in the Addo Elephant National Park and are a cause for concern.
7. Concepts of a balance of nature are outmoded.

8. Establishing a heterogeneous spatial template is more effective than continually counteracting change.
 9. Density feedbacks must ultimately curtail the growth in the elephant population.
 10. Further research needs to be focused most crucially on factors governing elephant movements and recruitment processes in savanna woodlands.
- In this context, we suggest the following considerations to guide management responses:

1. Since there is no easy solution, different measures need to be applied and tested through adaptive management.
2. Management should be spatially differentiated, and may involve zoning some areas as 'elephant sanctuaries' and others as 'tree sanctuaries' with clearly specified objectives.
3. Further research is needed to establish how elephants distribute their effects over space and the local conditions allowing tree regeneration to occur.
4. Reliable models of interactive ecosystem dynamics are required to project when threshold conditions of irreversibility are being approached.
5. Interventions may be needed to counteract likely lags in the elephant-woodland interaction, but with the need for action lessening as the size of the protected area gets larger.
6. It would be more effective, less costly and less contentious to establish a spatial template in order to restrict the extent of severe elephant impacts on vegetation, than continually to cull elephants.
7. Socio-political issues seem of more immediate concern than ecological ones, at least in the KNP.
8. The case for active intervention is stronger in smaller reserves, but other measures could reduce the need for culling.
9. Management interventions need to be backed by sufficiently informative monitoring of the consequences.

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1. Van Aarde R.J., Jackson T.P. and Ferreira S.M. (2006). Conservation science and elephant management in southern Africa. *S. Afr. J. Sci.* 102, 385-388.
2. Pienaar U. de V., Van Wyk P. and Fairall N. (1966). An aerial census of elephant and buffalo in the Kruger National Park, and the implications thereof on intended management schemes. *Koedoe* 9, 40-107.
3. Mills M.G.L., Whyte I.J., Viljoen A.J., Zambatis N. and Potgieter A.L.F. (1996). *Background information for the National Parks Board's review of the Kruger National Park's elephant management policy*. Scientific Report no. 1/96, National Parks Board, Pretoria.
4. Whyte I.J., Biggs H.C., Gaylard A. and Braack L.

- (1999). A new policy for the management of the Kruger National Park's elephant population. *Koedoe* 42, 111–132.
5. Whyte I.J. (2004). Ecological tests of the new elephant management policy for Kruger National Park and expected outcomes. *Pachyderm* 36, 99–109.
 6. SANParks (2005). *The Great Elephant Indaba held at Berg-en-Dal Conference Facility, 19–21 October 2004*. Online: <http://www.sanparks.org/events/elephants/report.pdf>
 7. Grant C.C. (ed.) (2005). A compilation of contributions by the scientific community for SANParks, 2005. *Elephant effects on biodiversity: an assessment of current knowledge and understanding as a basis for elephant management in SANParks*, pp. 158–212. South African National Parks, Skukuza: Scientific Services. Scientific Report 3/2005.
 8. Mabunda D. (2005). *Report to the Minister: Environmental Affairs and Tourism on developing elephant management plans for national parks with recommendations on the process to be followed*. SANParks, Pretoria. Online: <http://www.sanparks.org/events/elephants/>
 9. Havemann B. (2006). Major conservation NGOs feel action is needed in managing elephant numbers. *Afr. Wildl.* 60, 37–38.
 10. Van Wyk P. and Fairall N. (1969). The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* 12, 57–89.
 11. Caughley G. (1983). Dynamics of large mammals and their relevance to culling. In *Management of Large Mammals in African Conservation Areas*, ed. R.N. Owen-Smith, pp. 115–126. Haum Educational Publishers, Pretoria.
 12. Gillson L. and Lindsay K. (2003). Ivory and ecology — changing perspectives on elephant management and the international trade in ivory. *Environ. Sci. Policy* 6, 411–419.
 13. Leopold A.S. (1968). Ecological objectives in park management. *E. Afr. Agric. For. J.* 33, 168–172.
 14. Scholes R., Bond W. and Eckhardt H.C. (2003). Vegetation dynamics in the Kruger ecosystem. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, eds J.T. du Toit, K.H. Rogers and H.C. Biggs, pp. 242–262. Island Press, Washington, D.C.
 15. Gillson L. (2004). Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity* 1, 281–298.
 16. Biggs H.C. and Rogers K.H. (2003). An adaptive system to link science, monitoring and management in practice. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, eds J.T. du Toit, K.H. Rogers and H.C. Biggs, pp. 59–80. Island Press, Washington, D.C.
 17. Walker B.H. and Noy-Meir I. (1982). Aspects of the stability and resilience of savanna ecosystems. In *The Ecology of Tropical Savannas*, eds B.J. Huntley and B.H. Walker, pp. 556–590. Springer-Verlag, Berlin.
 18. Eckhardt H.C., Van Wilgen B.W. and Biggs H.C. (2000). Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *Afr. J. Ecol.* 38, 108–115.
 19. Dublin H.T., Sinclair A.R.E. and McGlade J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti–Mara woodlands. *J. Anim. Ecol.* 59, 1147–1164.
 20. Van Wilgen B.W., Govender N., Biggs H.C., Ntsala D. and Funda X.N. (2004). Responses of savanna fire regimes to changing fire-management strategies in a large African national park. *Conserv. Biol.* 18, 1533–1540.
 21. Prins H.H.T. and Van der Jeugd H.P. (1993). Herbivore population crashes and woodland structure in East Africa. *J. Ecol.* 81, 305–314.
 22. Walker B. (1989). Diversity and stability in ecosystem conservation. In *Conservation for the 21st Century*, eds D. Western and M. Pearl, pp. 121–130. Oxford University Press, Oxford.
 23. Wiseman R., Page B.R. and O'Connor T.G. (2004). Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *S. Afr. J. Wildl. Res.* 34, 25–37.
 24. Young T.P. and Lindsay K.W. (1988). Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *Afr. J. Ecol.* 26, 69–72.
 25. Brown P.M. and Wu R. (2005). Climate and disturbance forcing of episodic tree recruitment in a southwestern Ponderosa pine landscape. *Ecology* 86, 3030–3038.
 26. Skarpe C., Aarrestad P.A., Andreassen H.P., Dhillion S.S., Dimakatso T., du Toit J.T., Halley D.J., Hytteborn H., Makhabu S., Mari M., Marokane W., Masunga G., Modise S., Moe S.R., Mojaphoko R., Mosugelo D., Motsumi S., Neo-Mahupeleng G., Ramotadima M., Rutina L., Sechele L., Sejoe T.B., Stokke S., Swenson J.E., Taolo C., Vandewalle M. and Wegge P. (2004). The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33, 276–282.
 27. Leuthold, W. (1996). Recovery of woody vegetation in Tsavo National Park, Kenya, 1970–1994. *Afr. J. Ecol.* 34, 101–112.
 28. Herremans M. (1998). Conservation status of birds in Botswana in relation to land use. *Biol. Cons.* 86, 139–160.
 29. Parker I.S.C. (1983). The Tsavo story: an ecological case history. In *Management of Large Mammals in African Conservation Areas*, ed. R.N. Owen-Smith, pp. 37–50. Haum Educational Publishers, Pretoria.
 30. Western D. and Maitumo D. (2004). Woodland loss and restoration in a savanna park: a 20-year experiment. *Afr. J. Ecol.* 42, 111–121.
 31. Cumming D.H.M., Fenton M.B., Rautenbach I.L., Taylor R.D., Cumming G.S., Cumming M.S., Dunlop J.M., Ford G.A., Hovorka M.D., Johnston D.S., Kalcounis M., Mahlangu Z. and Portfors C.V.R. (1997). Elephants, woodlands and biodiversity in southern Africa. *S. Afr. J. Sci.* 93, 231–236.
 32. Rogers K. (2003). Adopting a heterogeneity paradigm. Implications for management of protected savannas. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, eds J.T. du Toit, K.H. Rogers and H.C. Biggs, pp. 41–58. Island Press, Washington, D.C.
 33. Gillson L., Lindsay K., Bulte E.H. and Damiana R. (2005). Elephants, ecology, and non-equilibrium? Response — we agree with Illius and Hamblin *et al.* *Science* 307, 674.
 34. Western D. (1989). The ecological role of elephants in Africa. *Pachyderm* 12, 42–46.
 35. Owen-Smith R.N. (1983). Dispersal and dynamics of large herbivores in enclosed areas: implications for management. In *Management of Large Mammals in African Conservation Areas*, ed. R.N. Owen-Smith, pp. 127–144. Haum Educational Publishers, Pretoria.
 36. Gaylard A., Owen-Smith N. and Redfern J. (2003). Surface water availability: implications for heterogeneity and ecosystem processes. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, eds J.T. du Toit, K.H. Rogers and H.C. Biggs, pp. 171–188. Island Press, Washington, D.C.
 37. Grainger M., Van Aarde R.J. and Whyte I. (2005). Landscape heterogeneity and the use of space by elephants in the Kruger National Park, South Africa. *Afr. J. Ecol.* 43, 369–375.
 38. Olff H. and Ritchie M.E. (1998). Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13, 261–265.
 39. Barnes R.E.W. (1982). Elephant feeding behaviour in Ruaha National Park, Tanzania. *Afr. J. Ecol.* 20, 123–136.
 40. De Beer Y., Kilian W., Versfeld W. and Van Aarde R.J. (2006). Elephants and drought changing woody vegetation in Namibia's Etosha National Park. *J. Arid Environ.* 64, 412–421.
 41. Owen-Smith R.N. (1996). Ecological guidelines for waterpoints in extensive protected areas. *S. Afr. J. Wildl. Res.* 26, 107–112.
 42. Guy P.R. (1976). The feeding behaviour of elephant in the Sengwa area, Rhodesia. *S. Afr. J. Wildl. Res.* 5, 55–64.
 43. Stokke S. and Du Toit J.T. (2000). Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography* 23, 70–80.
 44. Sinclair A.R.E. (2003). Mammal population regulation, keystone processes and ecosystem dynamics. *Phil. Trans. R. Soc. Lond.* 358, 1729–1740.
 45. Bell R.H.V. (1983). Decision-making in wildlife management with reference to problems of overpopulation. In *Management of Large Mammals in African Conservation Areas*, ed. R.N. Owen-Smith, pp. 145–172. Haum, Pretoria.
 46. Van Aarde R.J., Whyte I.J. and Pimm S.L. (1999). Culling and the dynamics of the Kruger National Park African elephant population. *Anim. Conserv.* 2, 287–294.
 47. Fowler C.W. (1981). Density dependence as related to life history strategy. *Ecology* 62, 602–610.
 48. Gough K.F. and Kerley G.I.H. (in press). Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: any evidence of density dependent regulation? *Oryx*.
 49. Laws R.M. (1969). Aspects of reproduction in the African elephant. *J. Reprod. Fert., Suppl.* 6, 193–217 mm.
 50. Dobson A.P. (1993). Effect of fertility control on elephant population dynamics. *J. Reprod. Fert. Suppl.* 90, 293–298.
 51. McNight B. (2000). Changes in elephant demography, reproduction and group structure in Tsavo East National Park (1966–1994). *Pachyderm* No. 29, 15–24.
 52. Owen-Smith R.N. (1988). *Megaherbivores. The Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge.
 53. Whyte I., Van Aarde R. and Pimm S. (1998). Managing the elephants of Kruger National Park. *Anim. Conserv.* 1, 77–83.
 54. Conybeare A. and Haynes G. (1984). Observations on elephant mortality and bones in water holes. *Quat. Res.* 22, 189–200.
 55. Dudley J.P., Craig G.C., Gibson D.St.C., Haynes G. and Klimowicz J. (2001). Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *Afr. J. Ecol.* 39, 187–194.
 56. Corfield T.F. (1973). Elephant mortality in Tsavo National Park, Kenya. *E. Afr. Wildl. J.* 11: 339–368.
 57. Caughley G. (1976). The elephant problem — an alternative hypothesis. *E. Afr. Wildl. J.* 14, 265–283.
 58. Baxter P.W.J. and Getz W.M. (2005). A model-framed evaluation of elephant effects on tree and fire dynamics in African savannas. *Ecol. Appl.* 15, 1331–1341.
 59. Hall-Martin A. and Modise S. (2002). *Status report: existing and potential transfrontier conservation areas in the SADC region*. Peace Parks Foundation, Stellenbosch.
 60. Harrington R., Owen-Smith N., Viljoen P.C., Biggs H.C., Mason D.R. and Funston P. (1999). Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Cons.* 90, 69–78.
 61. Pickett T.A., Cadenasso M. and Benning T. (2003). Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatio-temporal scales. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, eds J.T. du Toit, K.H. Rogers and H.C. Biggs, pp. 22–40. Island Press, Washington, D.C.
 62. Fayrer-Hosken R.A., Grobler D., Van Altena J.J., Bertshinger H.J. and Kirkpatrick J.F. (2001). Immunoneutralization of African elephants. *Nature* 411, 766.
 63. Mathews W.S. and Page B.R. (2005). The comparative use of woody species in different habitats by elephants in Tembe Elephant Park, Maputaland, Northern KwaZulu-Natal. In *A compilation of contributions by the scientific community for SANParks, 2005. Elephant effects on biodiversity: an assessment of current knowledge and understanding as a basis for elephant management in SANParks*, ed. C.C. Grant, pp. 128–131. South African National Parks, Skukuza: Scientific Services. Scientific Report 3/2005.
 64. Botes A., McGeoch M.A. and Van Rensburg B.J. (2006). Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biol. Conserv.* 130, 573–583.
 65. Kerley G.I.H. and Landman M. (2006). The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets. *S. Afr. J. Sci.* 102, 00–00.
 66. Redfern J.V., Grant C.C., Biggs H.C. and Getz W.M. (2003). Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84, 2092–2107.
 67. Whyte I.J. (2001). *Conservation management of the Kruger National park elephant population*. Ph.D. thesis, University of Pretoria.