DISCUSSION

Elephants, woodlands and ecosystems: some perspectives

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Introduction

My purpose in this article is to summarize, somewhat provocatively, the different perspectives that exist on 'the elephant problem'—that is, how might elephants and woodlands coexist? These perspectives range from viewpoints focused narrowly on the damaging effects of elephants on trees to broader considerations of the consequences for ecosystem processes and biodiversity. Furthermore, I will highlight the pivotal importance of spatial heterogeneity and the contribution of surface water distribution to this heterogeneity, because I believe that inadequate recognition has been given to this aspect in the past. For more detailed information, and complete referencing of information see Owen-Smith (1988), Gillson and Lindsay (2003), Skarpe et al. (2004) and Owen-Smith et al. (in press).

Public perceptions

To the public visiting parks and to the managers of these parks, elephants are vexing animals. They feed wastefully, breaking off branches to chew twig tips, stripping bark from tree trunks, and pushing over whole trees to sample a few bites from the top branches sometimes perhaps just to show their strength. They leave behind a trail of vegetation destruction: fallen trees, standing woodlands debarked and dead, magnificent trees like baobabs turned into a heap of sawdust, shrublands where once there were woodlands, and spreading grasslands where trees formerly grew. They are blamed for having destroyed most of the lush riparian forest that once flanked the Chobe River, and for transforming acacia trees in the adjoining woodland to standing skeletons amid a depleted shrubland dominated by *Capparis tomentosa*, *Combretum mossambicense* and *Croton megalobotrys*—species apparently unpalatable to elephants. Visitors to the park, tourist operators and many scientists generally view these vegetation changes as disturbing and regrettable. Furthermore, they are perceived as threatening the survival in the parks of other animal species, notably the Chobe subspecies of bushbuck.

A narrow ecological perspective

As they feed, elephants disturb the structural components of vegetation: they fell trees, uproot shrubs and pluck grass tufts whole. They depress or even eliminate populations of vulnerable tree species like baobab and marula. More broadly, they change the structure of the habitat for other species promoting less woody, more open conditions in savannas. By suppressing growth into canopy height classes, they make the woodland more shrubby to the detriment of birds requiring tall trees for nesting, like certain vultures and eagles. It has been claimed that they compete for food both with browsers like kudu and black rhinoceros, and with grazers like buffalo.

Adapted from the proceedings of a conference organized by the Botswana–Norway Institutional Cooperation and Capacity Building Project (BONIC), Vandewalle M, ed., *Effects of fire, elephants and other herbivores on the Chobe riverfront ecosystem*, Government Printer, Gaborone, 2003.

The concern of park managers is that a large elephant population will ultimately reduce habitat and species diversity, thus threatening the basic conservation objectives for protected areas. This was the justification for former culling programmes that capped elephant numbers in Kruger National Park in South Africa and Hwange National Park in Zimbabwe.

Broader ecological perspectives

Elephants as megabrowsers

All browsers to some extent affect plants negatively. Hares ringbark birch shrubs; steenbok, impalas and even rodents destroy tree seedlings; and outbreaks of defoliating insects like the spruce budworm can result in much tree mortality. The damage that elephants cause to individual plants, vegetation composition and structure is merely on a larger and more persistent scale, and thus more striking to human observers.

As expected from the niche theory, some degree of dietary separation is apparent between elephants and other browsers. Along the Chobe River front, kudus and impalas favour shrub species that elephants neglect. Thus some herbivores gain from the vegetation changes wrought by elephants, through complementary feeding habitats. Broader-scale habitat changes also benefit animal species favouring the new conditions, while other species lose out; thus an overall change in species numbers need not result.

Elephants as predators on woody plants

By definition predators are agents of the mortality of their prey. However, while individual animals or plants are killed, adverse changes in the abundance of the prey population need not result. Older individuals simply die sooner, opening opportunities for increased recruitment to fill the gaps and resources released. Nevertheless, there are circumstances in which vulnerable species may be held in 'predator pits' at greatly reduced density, or restricted to refuge habitats. A source-sink population structure may even develop, as indicated for baobab trees in the northern part of Kruger Park. Baobab stands on rocky hills, which elephants visit infrequently, show a wide range of sizes, while on the plains below there are isolated large trees but few saplings, suggesting that the plains subpopulation is maintained largely by seeds dispersed from the hills. Predation almost inevitably results in changes in the composition of the prey assemblage, with species robustly defended against predation increasing at the expense of those more vulnerable to being killed.

Elephants as agents of disturbance

Elephants can be viewed as agents of disturbance within plant communities through opening gaps for colonization where trees have been felled. According to the 'intermediate disturbance hypothesis', through creating such opportunities overall species diversity is enhanced, provided the disturbances are not too frequent or severe. Without disturbance, the most strongly competitive species eventually dominate the community. The vacant space generated periodically by the agent of disturbance enables pioneer species that are good colonists but not good competitors to coexist. Species diversity may be reduced within patches most heavily affected but over the landscape a mosaic diversity of habitats and associated species assemblages promotes higher diversity overall.

This concept implies that if there were too many elephants to the extent that their impact became persistent and pervasive over the landscape, plant diversity could be diminished due to the loss of species unable to resist such impact. On the other hand, too few elephants could also lead to lowered biodiversity following the disappearance of the gap colonists. Where lies the 'intermediate' abundance of elephants? We do not know at this stage and the question is not easily answered because diversity needs to be assessed at a variety of scales.

Elephants as ecological engineers

Elephants are supreme engineers in the sense that they radically transform their environment to suit their needs. In north temperate regions beavers are their counterpart, felling small trees to build dams, thereby flooding wetlands. Just as wildebeest cultivate grazing lawns in the Serengeti and white rhinos do likewise in Hluhluwe-iMfolozi, the impact of elephants feeding and breaking promote what might be called 'browsing lawns'. This term can be applied to the stands of small trees or shrubs 1–3 m tall—the ideal feeding height for elephants—that have developed on the Chobe alluvium and in mopane woodlands. Elephants prevent these plants from growing taller and hence out of reach by periodically breaking the leader shoot. Pushing over big trees, each of which may be replaced by several shrubs, is not as senseless as it may seem to narrow-sighted human observers. A parkland of widely spaced big trees is pleasing to humans but not productive for elephants. Other browsers may benefit through more accessible foliage, although the elephants may consume a good part of it.

Elephants as promoters of nutrient cycling

Mineral nutrients taken up by plants from the soil become locked in tree trunks and bark and thus are no longer available to support further plant growth. By pushing over trees, elephants help release these nutrients for recycling, thereby promoting further plant growth. The nitrogen held in elephant biomass may even be protected from the leaching that would otherwise take place in sandy soils, being released periodically in dung and urine. Places where elephants concentrate their effect thus become nutrient enriched and may develop into hotspots for other herbivores. These effects seem especially important in nutrient-deficient, sandy-soil ecosystems where elephants predominate in the herbivore biomass, like the Kalahari Sand region of northern Botswana and adjoining parts of Zimbabwe and Zambia. On the other hand, the loss of large trees removes the nutrient pumping role that these trees may have played, drawing mineral elements from deeper soil layers to counteract ongoing leaching of these nutrients from surface sands.

Dismal scenarios

What might the ultimate outcome of the effect of elephants on woodlands be? What form might the ecosystem eventually take? Here are four possible scenarios that would have deleterious consequences for biodiversity.

1. Elephants transform wooded savannas into open grassy savannas, especially on clay soil substrates, generally in association with fire. Thereafter the elephants suppress woody plant regeneration and species diversity is reduced as a result of the lack of the tree component. An example is the Rwindi–Rutshuru Plain in Virunga National Park, eastern Democratic Republic of Congo, which appeared as a wooded savanna in 1935 but had become an open grassland by 1959 (Bourliere 1965). Elephants also suppressed tree regeneration in the grasslands of the Masai Mara Reserve, although fire was implicated as the primary agent transforming the formerly wooded savanna into grassland (Dublin et al. 1990).
2. Elephants transform structurally mixed woodlands into monotonous shrublands, especially on sandy soil substrates. The elephants thrive but other organisms dependent on tall trees lose out, and structural diversity in the habitat is reduced. Tree populations may ultimately suffer from lack of seed inputs. This is the situation seen on the alluvial terrace adjoining the Chobe River and in mopane woodlands in some areas.
3. Elephants extirpate populations of vulnerable tree species like baobab, marula and various *Acacia* species, or at least restrict these at greatly reduced abundance levels in habitat refuges. Baobab trees have mostly disappeared from Tsavo East in Kenya and Gona-Re-Zhou in Zimbabwe. Nevertheless specimens of vulnerable species like *Acacia nigrescens* still persist along the Chobe River front, apparently resisting extirpation through their prickly defences. The woodland remains but becomes dominated by species not favoured by elephants.
4. Rather than attaining any stable state, elephant populations and woodlands cycle persistently, alternating between high and low abundance. This is Caughley's (1976) limit cycle concept, derived from observations made in mopane woodlands in Luangwa Valley. It may be expressed as a shifting patch mosaic across the landscape, with elephants abandoning places where the woody species they favour have become too sparse and moving into areas where plant populations have had time to recover, over time scales of centuries. With wide-scale movements by elephants now largely restricted by fencing and human settlements, the extreme swings could become worsened and prolonged with consequent losses of animal and plant species.

More optimistic scenarios

Recognizing the temporally highly variable environments that characterize much of Africa, it seems unlikely that any stable state would persist, not even the dynamic stability of a limit cycle. Instead populations of animals and plants must continually adjust to changing circumstances: seasonally, between wet and dry years, decades of above- and below-average rainfall, and to climatic shifts taking place over longer periods. This perspective of hierarchical patch dynamics is consistent with the vegetation changes revealed by fossil pollen records (Gillson 2004), and with observations of vegetation changes documented in Hwange over the past 30 years (Valeix et al. in press).

The fundamental contribution of spatial heterogeneity towards dampening the consequences of temporal variability for consumer–resource interactions is becoming widely recognized (Illius and O'Connor 2000; Owen-Smith 2002a,b). A crucial component of such heterogeneity in African savanna ecosystems is the restricted distribution of perennial surface water (Owen-Smith 1996).

With surface water restricted largely to rivers by the late dry season, riparian trees growing alongside these rivers incur the brunt of elephant impact. However, these species must also cope with periodic floods and hence should thus have the regenerative capacity to resist or counteract elephant-inflicted damage, for example by deep rooting. During the wet season when elephants can spread more widely across the landscapes, regenerative stages have the opportunity to recover. Variation in the persistence of ephemeral pools between years also affects the period over which elephants concentrate near rivers, providing further windows of opportunity for regeneration. Climatic variability could additionally enable the episodic establishment of dense cohorts of seedlings, providing 'herd' security against predation by elephants and other browsers.

Furthermore, elephants incur the stresses of daily movement between surface water and foraging areas several kilometres away where food resources are less severely depleted. The doubling in birth intervals and severe retardation of age at first reproduction documented in Uganda at Murchison Falls and in Kenya at Tsavo East (Laws and Parker 1968) occurred only after elephants had devastated woodlands and become severely stressed nutritionally as a result. With water restricted, young calves would suffer in particular from the cost of travel to and from water, and be susceptible to heightened mortality as a result. The crowding of elephants near water also increases the vulnerability of young elephants to predation by lions, as recorded in northern Botswana and Hwange (Joubert 2006). In combination, these changes could reduce to zero the annual 5–6% rate of increase now shown by many elephant populations. When the rains come elephants could spread widely across regions where food resources remain plentiful, so that the period of intense stress would be brief. Furthermore, with food abundant in these upland regions the pressure on tree species growing there would be reduced.

Conclusions

Narrow viewpoints emphasizing the necessity for population culling to restrict the severe effect that elephants can have on woodlands need not be applicable where ecosystems retain sufficient spatial heterogeneity. The problem is that managers have frequently intervened in ways that reduce this heterogeneity, for example by augmenting natural surface water with dams and boreholes. Furthermore, protected areas represent a circumscribed remnant of the range over which elephants moved in the past to exploit this heterogeneity.

Some intervention may be needed to restore or replicate the functional heterogeneity that may formerly have been effective within these areas. Where excessive artificial water points have been provided, as in Kruger, most should be closed. In Botswana where perennial water is restricted mostly to a few rivers, the temptation needs to be resisted to add boreholes to spread elephant impact. In Hwange, where available surface water is limited almost entirely to pumped pans, the distribution of these water sources needs to be restricted so as to concentrate the elephants while still providing sufficient access to water for other species (Chamaille-Jammes et al. in press). Such measures could be effective in dampening the extent of the fluctuations in the abundance of elephants and trees, thereby reducing the risk of species losses. The crucial question is, how large must the area be for these processes to operate unaided? To answer this, more information is needed on the factors governing elephant movements under different conditions, and on the processes governing the regeneration of savanna trees. It must be acknowledged that additional interventions may be needed in smaller protected areas to safeguard biodiversity objectives.

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References

Bourliere F. 1965. Densities and biomasses of some ungulate populations in eastern Congo and Rwanda, with notes on population structure and lion/ungulate ratios. *Zoologica Africana* 1:199–208.

Caughley G. 1976. The elephant problem: an alternative hypothesis. *East African Wildlife Journal* 14:265–283.

Chamaille-Jammes S, Fritz H, Murindagomo F. In press. Climate-driven fluctuations in surface water availability and the buffering role of artificial pumping in an African savanna: implications for herbivore dynamics. *Austral Ecology.*

Dublin HT, Sinclair ARE, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti–Mara woodlands. *Journal of Animal Ecology* 59:1147–1164.

Gillson L. 2004. Evidence of hierarchical pack dynamics in an East African savanna? *Landscape Ecology* 19:883–894.

Gillson L, Lindsay K. 2003. Ivory and ecology: changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy* 6:411–419.

Illius AW, O'Connor TG. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89:283–294.

Joubert D. 2006. Hunting behaviour of lions on elephants in the Chobe National Park, Botswana. *African Journal of Ecology* 44:279–281.

Laws RM, Parker ISC. 1968. Recent studies on elephant populations in East Africa. In: MA Crawford, ed., *Comparative nutrition of wild animals*. Symposium of the Zoological Society of London No. 21. p. 319–359.

Owen-Smith N. 1988. *Megaherbivores: the influence of very large body size on ecology.* Cambridge University Press, Cambridge, UK.

Owen-Smith N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research* 26:107–112.

Owen-Smith N. 2002a. Credible models for herbivore-vegetation systems: towards an ecology of equations. *South African Journal of Science* 98:445–449.

Owen-Smith N. 2002b. *Adaptive herbivore ecology:.from resources to populations in variable environments.* Cambridge University Press, Cambridge.

Owen-Smith N, Kerley GIH, Page B, Slotow R, van Aarde RJ. In press. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*

Skarpe C, Aarestad PA, Andreassen HP, Dhillion SS, Dimakatso T, du Toit JT, Halley DJ, Hytteborn H, Makhabu S, Mari M et al. 2004. The return of the giants: ecological effects of an increasing elephant population. *Ambio* 33:276–282.

Valeix M, Fritz H, Dubois S, Kanengoni K. In press. Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology.*