The Ecological Role of Elephants in Africa

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Elephants can be considered in many ways: economically, culturally, symbolically, aesthetically, educationally and scientifically, to mention the most common. Another kind of value judgment is the ecological. There are two problems with ecological arguments for conserving species. First, the ecological details are seldom obvious to anyone but an ecologist, and second, it is difficult to show the consequences of losing a species until after the species is extinct.

This is not to say that predictions about the outcome of extinctions are lacking. A growing number of ecologists are pointing out the likely consequences in the coming decades of losing species. These projections are necessarily generalities and have little to say about specific effects due to losing say the giant panda or the black rhino. None the less, the science of conservation biology, drawing on knowledge of the roles played by predators, pathogens, pollinators, seed-dispersers and so on, is improving its forecasts. Certain "keystone" species play an inordinate role in maintaining the linkages in a food web, to the extent that their extermination would cause a cascade of change or extinctions in ecosystems.

What of the elephant? Can we predict the consequences of its extinction or near eradication in Africa? Most of the early studies of the effects due to elephant were conducted in national parks, where densities were unusually high due to range compression, or in commercial forests, such as Budongo in Uganda. Not surprisingly these studies stressed the negative impact of elephants — a reduction of biological diversity in parks and an economic loss of timber in forests. In contrast, more recent studies stress the importance of elephants as agents of seed dispersal, in increasing habitat mosaic in forests and in diversifying mammalian communities.

These views of the ecological role of elephants are not necessarily contradictory. The issue revolves round whether elephants are free-ranging or compressed by human pressures. I will give a number of examples of the keystone role of elephants in African ecosystems, drawing on firm evidence from natural "removal experiments", supported by other evidence. This will lead to a discussion of the ecological implications of losing elephants using the analogy of mega-faunal extinctions in Central American dry forests and the cascade of Pleistocene extinctions recently attributed to the loss of large mammals between 25,000 and 10,000 years ago.

Elephants and Savannas

A compelling example of what happens to biological diversity when an area is void of elephants comes from Amboseli in Kenya where poaching has produced a natural removal experiment. Prior to 1950, elephant numbers in the Amboseli basin, the focus of wildlife concentrations during the dry season, were low. The evidence suggests elephants were scarce in Amboseli late last century, perhaps due to ivory trading, and increased steadily through the early decades of this century. Elephants migrated seasonally in and out of the basin, like most other herbivores, until the mid-1970s when poachers killed more than a third, causing the remaining animals to concentrate in the national park, the dry season range. Here their concentration increased several-fold. The contraction in range led to a density gradient within the formerly uniform woodlands of the Amboseli basin, with extremely high densities in the national park falling away to negligible levels beyond the park boundary. What were the consequences for vegetation? Both the number and relative abundance of plant species were affected. Comparably few plants, dominated by one or two species, are located in areas of low to negligible elephant density and in the central park, where elephant densities are exceptionally high (more than 4 per sq. km.). Conversely, two or three times as many species, contributing far more evenly to total plant abundance, are found in areas of moderate elephant density. What does this pattern mean?

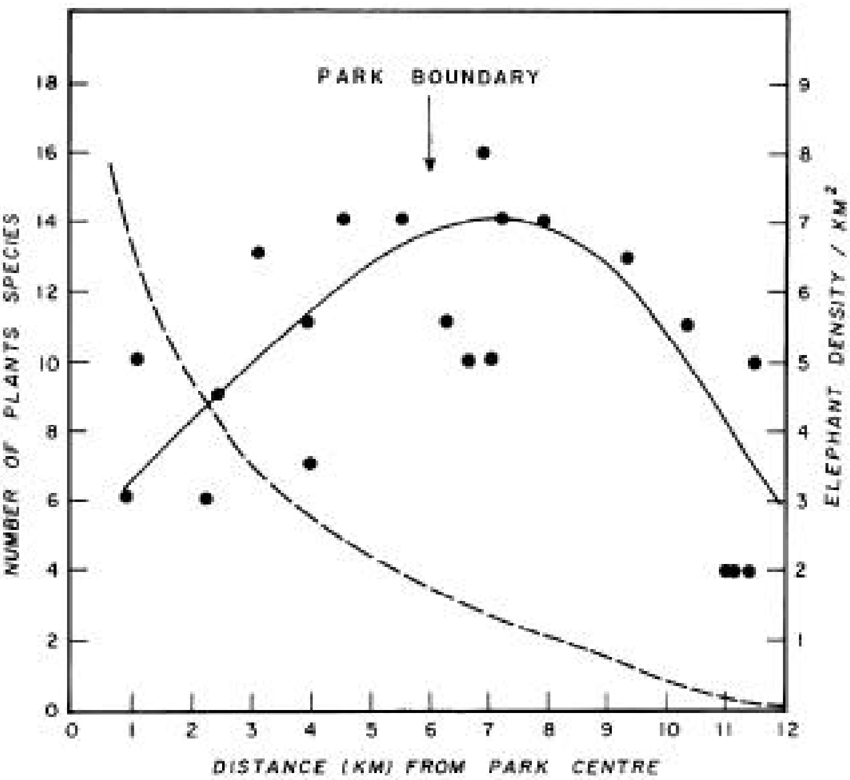

__Fig. 1.__ Plot of the number of plant species (—) along an elephant density gradient, (—) in Amboseli. Most species are Pound in areas of intermediate elephant density, fewest in areas where elephants have been compressed or eliminated.

With few elephants present, the basin vegetation be-comes dominated by one species, the yellow-barked acacia, a fast growing tree forming dense stands over *25* m tall. Woodland groves become so dense that little light penetrates to the understorey, and consequently a few species of light tolerant herbs invade the woodland floor. Unlike moist tropical forests, only a few aridadapted plants, narrow leaved to withstand desiccation, can tolerate deep shade. The presence of elephants in moderate numbers opens up the dense woodland canopy, allowing a proliferation of species in the light gaps. The invading species, including shrubs, herbs and grasses, in turn reduce the germination rate of fever trees, reducing their domination.

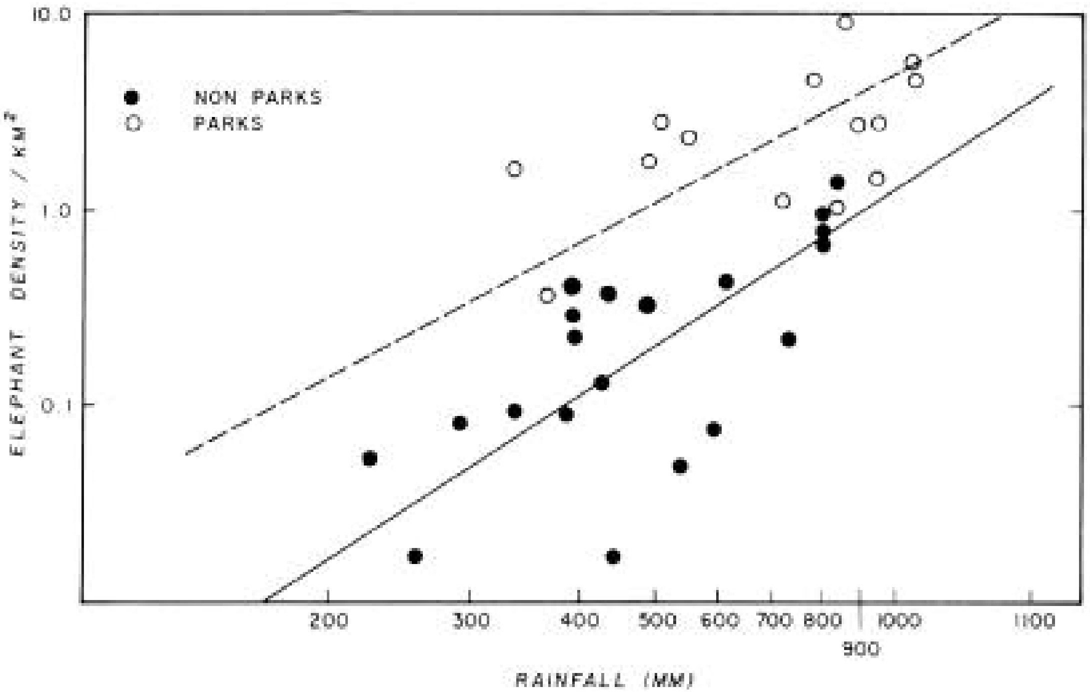

Fig. 2. *Elephant biomass for 34 East African populations showing a five-fold difference between non-parks and parks, a reflection of the push-pull effect of vulnerable and protected areas.*

This pattern is perhaps typical of much of the savannas where elephants, until recent years, lived in moderate densities, moved widely and were frequently edged on by hunters, pastoralists and shifting cultivators. The exceptional concentrations in the central Amboseli are historically unprecedented in dry areas. Here the year-round densities within the woodlands exceed *3.5* per sq kin, and in the core area exceed 6 per sq kin, figures higher than compressed populations in far wetter areas such as Murchison Falls Park in Uganda. The present densities in Amboseli did not prevail in the past when elephants had the chance to move uninterruptedly.

Elephants, in modifying Amboseli's vegetation, also indirectly shape its wildlife community. The following analysis is a preliminary summary of the results from the long-term census records.

Census results from aerial counts show significant increases in grazer biomass (zebra, wildebeest, Thomson's gazelle and buffalo) and decreases in browser and mixed feeder biomass (giraffe, impala, Grant's gazelle) within the park where elephants have reduced the woodlands and swamp-edges, and expanded grasslands. A reverse decrease in grazer biomass and increase in browser biomass has occurred where woodlands have proliferated outside the park. The most equitable mix of grazers and browsers is found in the mosaic of woodlands and grasslands associated with moderate elephant densities straddling the park boundaries.

Other Savanna Examples

Woodlands and bush-land are the dominant feature of the African savannas, contrary to the popular image of open plains. In the absence of cutting, burning and elephants, grasslands often give way to dense bush-land. Elephants can reverse such encroachment, as seen in Tsavo, Kruger and Ruaha, an event that favours grazing animals and often increases overall animal production. Many commercial ranches, such as Galana and Laikipia in Kenya, owe much to elephants.

Elephants also "facilitate" pastures for other species including livestock, whether or not tsetse are present. Vesey-Fitzgerald in 1960 described how elephants and other large herbivores opened up floodplain marshes to an array of medium and small ungulates in Lake Rukwa, Tanzania. I have also described how elephants in Amboseli open up swamp and swamp-edge pastures to other herbivores, including domestic stock, by feeding on and trampling down tall sedges, and promoting growth of higher quality grasses. This phenomenon is undoubtedly widespread, especially in the single rainfall belt of central Africa and Sudan, where grass grows *3* to 4 m tall and becomes rank and unpalatable for smaller herbivores, unless grazed down or burned.

Given the widely accepted view that bio-diversity is the primary goal for biological conservation, there are firm ecological grounds for concern over the current status of elephants in the savannas. From the observation that savanna ecosystems are least diverse at low and high elephant densities, one can argue that the savannas are already becoming simplified on a large scale. This deduction can be made from the skewed distribution

Elephants in Queen Elizabeth National Park, Uganda

quarter of the lowland forest birds in sub-Saharan Africa are secondary forest and forest-edge species. Elephants, the giant bulldozers, no doubt have done much to create the patchiness that distinguishes African from South American forests.

The extent to which elephants create or simply expand forest gaps is not yet clear. At low densities they are unlikely to have much influence in gap formation. At high densities elephants have a profound influence in creating secondary forests such as Aberdares, Lake Manyara and Rubondo. However, most of these cases reflect compressed elephant populations which, as in over-populated savanna parks, reduce the variety of plant species. Nevertheless, elephants have a pervasive influence throughout the central African forest and probably play an important role in the formation and maintenance of their patchy nature.

of elephants (Fig. 2). Elephants cluster into two discrete classes — high and low density — with very few in the intermediate range. The two classes correspond to parks and non-parks, to those areas where elephants concentrate for safety, and those where they flee from human threats, largely poaching. Both parks and non-parks are likely to lose diversity as a result, the first from too many elephants, the second from too few.

What little we know about the ecological role of elephants in forests suggests that they play a similar role in the savannas, as the following examples show.

Elephants are important agents of seed dispersal. Alexandre, in 1976, found 21 of 71 species he sampled in Tai Forest, Ivory Coast, were adapted to dispersal by elephants. Elephants are obligatory dispersers for a number of trees, especially those with large tough seeds, implying that these species will dwindle in number once elephants are exterminated.

Elephants play a second and equally essential role in creating forest gaps. The formation of gaps by tree falls, wind-throw and other natural factors helps to diversify tropical forests. The upper canopy layers intercept so much light that little reaches the forest floor. Understorey vegetation is therefore sparse, a fact reflected in the low abundance variety of vertebrates on the forest floor. Elephants create and expand gaps and, in the process, open up a more productive and varied ground layer to a range of other vertebrates, including gorillas, forest hog, bush pig, bongo, buffalo and duiker. The high proportion of gap and secondary forest species of plants and animals in African forests suggests its patchiness is a natural feature. Over a third of the plants in Ghanaian forests are secondary forest species and a

Primatologist Kortlandt holds a similar view. He speculates that the monotonous architecture and species-poor forests of central Congo Basin reflects ‘the absence of rejuvenation owing to the extermination of elephants”. By implication, the elimination of elephants in the rich African forests will lead to faunal impoverishment.

Conclusions

Elephants play a previously overlooked keystone role in African savannas, and almost certainly tropical forests too. To some extent their diversifying role has been obscured by a preoccupation with over-browsing in national parks, where elephant populations have been compressed by human activity. The evidence at hand suggests that elephants diversify savanna and forest ecosystems when free to move. Unfortunately, heavy poaching and harassment is producing a split distribution of high and low densities over much of Africa as herds crowd into protected areas and abandon nonprotected lands.

Elephants also stem bush invasion in savanna ecosystems and dry forests over much of Africa, thereby creating a more productive mix of grazing and browsing animals. Subsistence herders and commercial ranchers also benefit when elephants reduce bush-lands, expand grasslands and eliminate tsetse fly. The ecologically diversifying role of elephants in the savanna,

COMPARISON OF ESTIMATED AFRICAN ELEPHANT POPULATION SIZES BETWEEN 1979 AND 1989 BY COUNTRY WITHIN REGION

Country by Region	1979 [1]	1989 [2]
Central Africa		
Cameroun	16,200	21,200
Central African Republic	63,000	19,000
Chad	15,000	3,100
Congo	10,800	70,000
Equatorial Guinea	1,300	500
Gabon	13,400	76,000
Zaire	377,700	85,000
Subtotal	497,400	274,800
Eastern Africa		
Ethiopia	900	6,650
Kenya	65,000	19,000
Rwanda	150	70
Somalia	24,300	6,000
Sudan	134,000	40,000
Tanzania	316,300	80,000
Uganda	6,000	3,000
Subtotal	546,650	154,720
Southern Africa		
Angola	12,400	12,400
Botswana	20,000	51,000
Malawi	4,500	2,400
Mozambique	54,800	18,600
Namibia	2,700	5,000
South Africa	7,800	8,200
Zambia	150,000	41,000
Zimbabwe	30,000	43,000
Subtotal	282,200	181,600
West Africa		
Benin	900	2,100
Burkina Faso	1,700	3,900
Ghana	3,500	1,100
Guinea Bissau	-	20
Guinea	300	300
Ivory Coast	4,000	3,300
Liberia	900	650
Mali	1,000	600
Mauritania	160	20
Niger	1,500	800
Nigeria	2,300	3,100
Senegal	450	50
Sierra Leone	300	250
Togo	80	100
Subtotal	17,090	16,290
TOTAL	1,343,340	627,410

Sources: 1. Iain Douglas-Hamilton (1979)
2. Ivory Trade Review Group Report (1 989)

coupled with their economic importance is reason to encourage their range expansion beyond protected areas. This would avoid the loss of biological diversity due to over-compression within protected areas and enhance it outside in areas where livestock grazing encourages bush encroachment.

Seen in larger context, the implications of losing elephants may be far-reaching in the long run. Janzen and Martin in 1982 suggested that the mega-faunal extinctions in the late Pleistocene resulted in a loss of dispersal agents for a number of tree species in the Central American dry forest, leading to habitat impoverishment. Janzen made a similar case for the drier rangelands of Central America and the Southwest United States, where plants resilient to browsing by smaller herbivores have proliferated since the extinction of the mega-fauna.

We can expect the loss of elephants in Africa to have equally wide ranging consequences. Owen-Smith has advanced the "keystone herbivore hypothesis" to account for the cascade of extinctions among smaller mammals during the Pleistocene, which saw 50% of the mammalian genera disappear. In noting that all species larger than 1,000 kg disappeared in the Americas, Europe and Australia between 25,000 and 10,000 years ago, he suggests that hunting, while a good explanation of the mega-mammal extinctions, fails to explain the simultaneous loss of 41% of the meso-mammals (between 5 and 100 kg) and 2% of micro-mammals (less than 5 kg) that were not obvious prey of early human hunters. He suggests instead that the extermination of the mega-mammals led to a domino effect as vegetation closed up and eliminated the habitat of smaller mammals. He cites Hluhluwe Game Reserve in South Africa as a modern analog. There, since the elimination of elephants a century ago, the local extinction of three grazers and the sharp reduction of several others, such as waterbuck and wildebeest, to vulnerable levels has coincided with the invasion of woody vegetation.

In conclusion, the case studies and the ecological and palaeoecological literature suggest that the extermination of the African elephant will reduce biological diversity and increase extinction rates over much of Africa. Lose our keystone species and we will lose a great deal more in the process.