

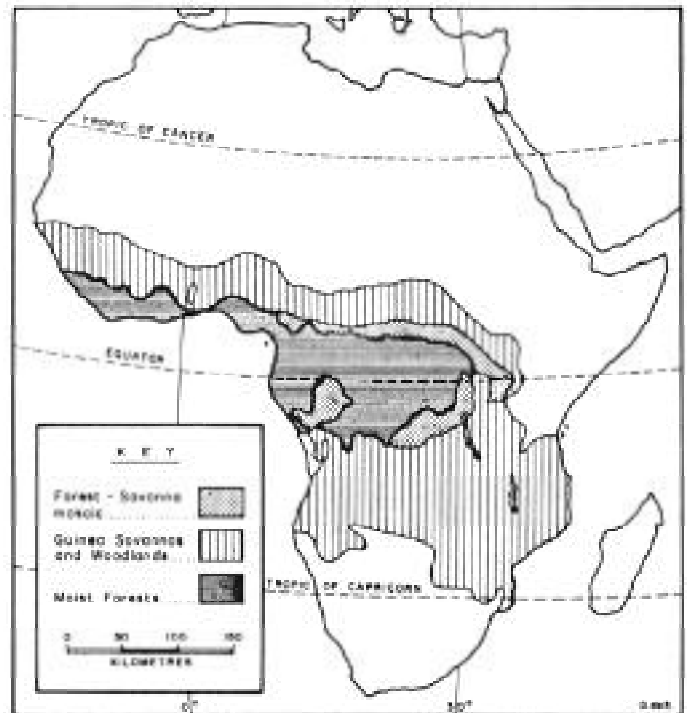
Why do Elephants Destroy Woodland?

Since the onset of colonial contacts in the last century, a fundamental change in land use patterns and life styles has taken place in Africa. The human population has increased manifold and most parts of Africa now consist of human settlement surrounding a few islands of wilderness, which are maintained by force of legislation in the form of conservation areas. Over the past forty years, elephant numbers have been rapidly increasing in some of these conservation areas, firstly as a result of law enforcement, secondly as a result of immigration of elephants from areas progressively settled outside and, thirdly as a result of Park management in the form of installation of artificial water supplies (i.e. Wankie National Park, Zimbabwe; Kruger National Park, South Africa and Tsavo National Park, Kenya). The massive build-up of elephant numbers was followed by a decline in woodland density due to a combination of tree destruction by elephants and burning (Laws, Parker & Johnstone, 1975; Caughley, 1976; Barnes, 1980 and Lewis, 1982). In a number of Parks this has led to the disappearance of large areas dominated by *Acacia* and *Commiphora* woodland and local extinction of tree species like Baobab (*Adansoni digitota*), which is highly favoured by elephant. The elephant were not capable of responding to these self-inflicted radical changes in the food supply, firstly because migration to better feeding grounds was usually difficult on account of human settlement and illegal activity and secondly because changes in the reproductive rate have a time lag (t) with a length equal to the age at onset of reproduction. Even if infant mortality would increase to a full hundred percent, the size of the breeding segment of the population would continue to increase for a period equal to the time lag (t), without significant changes in the calving interval and age at attainment of sexual maturity (Jachmann, 1984a & b). For these reasons it is not advisable to pursue a 'laissez-faire' management under conditions of elephant overabundance. After a long period of drought in 1972, laissez-faire management in the Tsavo National Park led to heavy mortality of elephants of all age-classes. In other Parks in Africa the culling of elephants was annually carried out as a management practice and appeared to be successful (Wankie - now known as Hwange -and Kruger National Parks).

We have now reached the point where we ask if modification of woodland by elephant is a natural phenomenon that is part of a cyclical relationship always existing between woodland and elephants (Caughley, 1976) or, if true equilibria between woodland and elephants are indeed possible under some ecological conditions. The installation of artificial waterholes and compression of elephants into sanctuary areas may be factors contributing to the rapid decline in woodlands. However, other factors are likely to be involved, while the causes differ depending on the type of habitat.

In this short contribution we suggest that a major factor contributing to habitat degradation by elephant is a maladapted feeding strategy, as most of the present-day elephant populations in Africa probably have evolved in the moist forests and Guinea woodlands of Central Africa. In order to clarify this hypothesis we shall first examine elephant feeding behaviour.

Tree utilisation



Utilisation of trees by elephant can be subdivided into five main categories: (i) consumption of fruits, (ii) defoliation and breakage of twigs and branches, (iii) debarking and consumption of woody material of the trunk, (iv) consumption of roots and, (v) breakage and pushing over of the tree. Depending on the amount of damage, both the third and fourth categories may be fatal to the tree in combination with fire, while the fifth category will definitely kill the tree. This last category is most interesting as the action does not usually provide the elephant with extra food he would have been unable to obtain without destruction of the tree, while in addition, the tree is lost for future foraging. According to Douglas-Hamilton (1972), Croze (1974) and Guy (1976), the uprooting and pushing over of trees by elephant is more a social display than a feeding necessity. However, in Kasungu National Park, Malawi, the felling of trees by elephants appeared to be part of a feeding strategy that leads to increase of browse production of preferred height-classes and of preferred species and materially improves the availability of food for elephants during the dry season (Jachmann & Bell, unpublished; Jachmann, 1984b). It has also been shown by other workers in this field (cf Olivier 1978) that the successional climax of a woodland or forest is certainly not the most productive stage and that food availability for elephant can be as much as factor 2.6 times higher in secondary rainforest as opposed to primary rainforest (Olivier, 1978).

The vegetation of Kasungu National Park is predominantly composed of *Brachystegia* woodlands (Guinea woodlands). Guinea savannas and woodlands, dominated over wide areas by *Brachystegia*, *Julbernardia* and *Isobertia* trees, are situated on the ancient and infertile soils of the Central African plateau and support low elephant densities. As pointed out by Bell (1981a), the conditions under which elephants are likely to have a substantial impact on the vegetation (in the absence of

poaching) are those that favour both tree and elephant production, i.e. soil conditions of medium to high nutrient status and high infiltration rates favouring plant biomass production. The soil-water dynamics of Guinea woodlands generally favour plant biomass production; however, the low nutrient status of the soils effects a low level of feeding efficiency and inhibits production of higher trophic levels. In Kasungu National Park, total rainfall (about 800 mm/year) and soil-water dynamics effect a high rate of coppicing when trees are killed by elephant and fire, resulting in a dense coppice regeneration, which is found to be an equilibrium phase of *Brachystegia* woodland (Bell 1981b). However, under semi-arid conditions, in areas where soil-water dynamics favour grass growth, the coppicing rate is likely to be low, while in addition fires are hot due to grass biomass and woodland areas may be modified by elephant (i.e. Sudan savannas and woodlands dominated by *Acacia* and *Commiphora* species). In certain Rift Valley areas like the Luangwa valley in Zambia, the production of all trophic levels is extremely high and local overabundance of elephants results in the disappearance of certain highly favoured tree species like Baobab, without intensive modification of large areas of the habitat (with the exception of some of the mopane woodlands).

Early over-exploitation of Africa's elephant population

The figure shows the moist forests of Central Africa, the Guinea savanna and woodland belt and an intermediary vegetation zone of forest savanna mosaics. The figure is a generalization as it does not show the montane habitats and Rift Valley areas, while the Guinea belt is actually a mosaic of savanna and woodland areas. About 60-70% of the elephants in present-day Africa occupy the moist forests and Guinea belt of the central part of the continent (after I. Douglas-Hamilton, 1979). Another approximately 5% occupies Rift Valley areas situated within this region, like the Luangwa and Zambezi valleys in Zambia and Mozambique. Intensive habitat modifications by elephant have been reported for a number of areas, mostly situated outside the moist forests and Guinea belt.

If we go back to the 17th century when large scale elephant hunting for ivory started, we see that large populations were eliminated over wide areas (Spinage, 1975). As the ivory had to be hauled overland by foot or by pack-animals, intensive exploitation of elephant populations started in the coastal regions and approximately halfway through the 19th century, elephants had been exterminated over large areas of West Africa and Africa south of the Zambezi (Spinage, 1975). By the end of the 19th century, elephants were completely absent from extensive areas of East Africa where the Arabs had control over the ivory trade (Spinage, 1975). Elephant hunting in Central Africa was less intensive, because the ivory had to be transported over vast distances to reach the coast, while in addition the region was less accessible than the largely open areas of southern and eastern Africa. The moist forests of Central Africa were occupied by the somewhat smaller forest elephant, while the eastern and southern regions bordering on these forests were most likely occupied by populations with a large degree of interbreeding between the savanna and forest elephant. During periods of over-exploitation of elephant populations in East and South Africa, the process of elephant dispersal was accelerated, while the

Central African population acted as the centre from where migration took place. We would like to suggest that the majority of present-day elephant populations occupying eastern and southern Africa are descendants from this main Central African population, implying that the feeding behaviour of these elephants is similar to that of the elephants currently occupying the moist forests and Guinea belt of Central Africa. If this assumption is true, the destruction of woodland by elephant would not only be due to overabundance in combination with fire and management actions, but also to a maladapted feeding strategy. Undoubtedly, the compression of elephant in combination with the time lag effect in the reproductive rate play an important role in the modification of habitats. Cyclic relationships between trees and elephants, if existing at all, are likely to be masked by trends in elephant hunting over the past centuries (Spinage, 1975).

Conclusion

Increasing browse availability following pushing over of trees is a feeding strategy which is appropriate to moist oligotrophic woodland and forest. This strategy may be of general significance in the evolution of elephant ecology. The majority of African elephants live in the moist oligotrophic biome, while the remaining animals are most likely descendants from this central African population. This implies that the elephants causing the classic management problems as to modification of the habitat may be a maladapted minority.

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