

Elephants and Woodlands II

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A brief article on elephant/woodland interactions, published in the AERSG newsletter (Jachmann and Bell, 1984) has generated a lively discussion on elephant feeding strategies and on the equilibria between elephants and their food sources (Lindsay and Olivier, 1984; Bell, 1985; Lindsay, 1987). Although I feel that, at this point, the dialogue seems primarily to concern semantic issues, I would like to clarify and expand some of my ideas on these topics. The various arguments will be treated separately below.

ELEPHANT DIETARY REQUIREMENTS

In his last response, Lindsay (1987) addresses the question whether elephants are primarily grazers or browsers, probably misunderstanding the essence of our point in Bell's reply (1985). Once more I would like to make it clear that the information available shows that elephants require a diet consisting of at least 50% browse on a year-round basis. This observation results from the simple fact that in any given situation grasses rapidly become too fibrous (thereby decreasing their digestibility and diluting the nutrients present) to make up a substantial part of an elephant's diet for an extended period. Furthermore I do not believe that it is correct to state that the "cell walls of grasses are not highly lignified" (Lindsay, 1987). As compared to what? In comparison with woody browse, but certainly not with foliage; firstly, because "not highly lignified" only applied to a relatively short period and secondly, grass lignins differ from browse lignins in structure and/or in composition (Swain, 1979). Browse and grass species with a similar lignin content may show a difference in digestibility (by reducing the availability of carbohydrates and proteins to herbivores) in favour of browse species. Moreover, the lignin content of grasses between 2% and 8% dry weight (Soest and Wine, 1967) – is the same as that of the foliage of the *Brachystegia* woodlands (miombo) of Kasungu National Park, Malawi, also containing between 2% and 8% lignin, i.e. 4.74 ± 1.73% in the early wet season (Jachmann, in prep.). The lignin content of miombo leaves slowly increases over the seasons by about 1%, whereas the lignification process in grasses takes place more rapidly and to a greater extent. By reducing overall digestibility, lignins appear to be an important factor determining selective feeding by elephants (Jachmann, in prep.). A certain amount of crude fibre (cellulose and hemicellulose), however, appears to be an essential component of an elephant's diet (Jachmann, in prep.). A high protein/fibre ratio, as in young grasses, may give a rapid throughput and a low absolute rate of assimilation (R.H.V. Bell, pers. comm.) necessitating the intake of a certain amount of browse. In addition, for a given area, the concentration of minerals like magnesium, calcium and sodium may be two to four times lower in grasses than in browse, on a year-round basis (Dougall et al., 1964). It was shown by Jachmann (1983a, 1985 and in prep.) that these minerals significantly contribute to the selective utilisation of browse species by elephants in the miombo woodlands of Malawi.

WOODLAND RESPONSE TO ELEPHANT DAMAGE

Plant secondary chemicals may be important factors, both in contributing to the relative instability of woodlands in arid eutrophic areas under the influence of elephant feeding and in promoting the existence of equilibria between coppice phase woodlands and elephants in moist oligotrophic areas. As shown by Waring et al. (1985), carbon-based defensive compounds such as tannins increase with a decreasing nutrient availability. In Kasungu National Park, tree species growing in "valley areas" with a relatively high soil nutrient status exhibit low levels of phenolic compounds compared to those species growing on the infertile "plateau areas" (Jachmann, unpubl.). In general, trees growing on eutrophic soils may exhibit relatively low levels of carbon-based defensive compounds as compared with trees growing on oligotrophic soils.

Tree foliage of the Kasungu miombo woodlands varies in total phenolic content from 1 to 16% dry weight (Jachmann, in prep.), whereas the protein precipitating capacity varies from 0 to 1 mg protein per mg of dried plant material. The threshold values, at which elephants avoid feeding on the tree, are about 100/a total phenolics with a protein precipitating capacity of about 0.5 mg protein per mg dried plant material. South African researchers have shown that after a tree has been damaged by browsers, the tannin-C content (proanthocyanidins) of several miombo species increases by as much as three times within a period of only one hour – after which several species sustained a relatively high tannin-C level for a couple of days (van Hoven, 1985).

Acacia tortilis, a species mainly occurring in arid eutrophic areas and very susceptible to elephant attack, not only increased phenolic content from a low basic level of 2.3% to 3.3% in one hour (43%) but also showed a rapid decrease back to its normal level. Apart from the fact that miombo tree species have a high basic level of phenolic compounds, the extent to which the increase in these occurs as well as the period of decrease probably differ from species found on richer soils. This implies that in areas with predominantly miombo woodland and relatively high elephant densities, in addition to other secondary chemicals, a large number of trees will have a phenolic content exceeding the threshold value for elephants. Mature trees however, with a canopy above the maximum feeding level for elephants, will not be damaged up to the moment until the tree is pushed over. Although the protein/fibre ratio of such a mature tree may be lower than that of its coppice neighbour, other components may occur in similar concentrations and the phenolic content will be relatively low (Jachmann, in prep.).

Hence, depending on the conditions, the short term benefit of feeding on foliage with low levels of phenolic content seems to be more important than the longer term advantage (side effect) of stimulating grass production and/or enhancing the occurrence of coppice phase trees in miombo woodlands. We could say that the direct feeding necessity is the proximate causal factor that brings about the tree felling behaviour.

Activity areas of family units and entire kin groups, however, appear to be relatively stable, depending on the human/animal conflict situation (Jachmann, 1983b). In combination with the long lifespan and social organisation of elephants, there appear to be conditions under which the effect of the long term advantage of the tree felling behaviour should not be underestimated. As pointed out by Bell (1985), the Namibia desert elephants utilise trees on a sustainable basis. This shows that in arid conditions, the negative long term effect is strong enough for the "minimal damaging trait" to penetrate the population and in the long run outweigh the short term benefits.

Certain tree species in arid eutrophic areas may have relatively low basic levels of phenolics. Moreover the phenolic content cycle, occurring after damage inflicted by herbivores, may generally take place within a relatively short period. This implies that herbivores can browse on a single tree with its canopy within feeding range during a relatively long period. Other tree species may show a similar severe response in phenolic activity as those found in miombo woodlands.

Instability of woodlands in arid eutrophic areas, however, is the outcome of interactions between a large number of factors, several of which will be briefly outlined below:

1. Growth and regeneration

1.1 Seed germination: Seeds are often highly nutritious and low in defensive compounds (*Acacia*), encouraging utilisation by beetles and monkeys amongst others. Rainfall and soil infiltration rates are low, resulting in low water potentials, inhibiting seed germination.

1.2 Growth is affected by the large biomass of other browsers causing a vast amount of damage to seedlings and saplings, whereas in some areas the grass biomass results in hot fires, increasing the probability of death in the youngest trees. The growth of saplings and seedlings is also inhibited by low water potentials.

1.3 Regeneration of trees after breakage by elephants may follow a species dependent pattern. A dominating top meristem in combination with a relatively small tap-root in certain **Acacia** species may inhibit multi-stemmed coppicing and the growth of side branches (Jachmann, unpubl.).

2. The density of trees seems to follow an inverse relationship with the soil nutrient availability.

3. Shade intolerance in certain tree species will select for height growth rather than strength and longevity, resulting in a relatively thin stem and a heavy canopy in mature trees. The tree will be easy to push over, even at higher ages (low safety factor).

4. Factors inherent to the animal populations, like the time lag in reproductive response in elephants. This is, however, beyond the scope of this contribution.

Although basic levels and cycles in phenolic activity may significantly contribute to woodland instability under the influence of herbivores, another phenomenon may also be involved. In arid eutrophic areas, high densities of browsers, a minimal coppicing rate and slow regeneration in a number of tree species may be major factors contributing to a possible shift of a large part of the tree canopy to levels above the feeding range for elephants, necessitating tree felling to bring the biomass within reach.

THE NON-DAMAGING TRAIT IN THE NAMIBIA DESERT ELEPHANTS

Why did this non-damaging trait evolve under these particular conditions and not elsewhere? Significant factors may be the size and location of the seasonal activity areas of the units of the various kin groups that belong to a clan. The size of an area depends on the number of animals in the unit, due to food competition ($P < 0.001$; Jachmann, 1983b). The size, location and overlap of activity areas also depend on the food availability at that particular time of year (Jachman, 1983b). In Kasungu National Park, dry season activity areas are mainly located in the "plateau" woodlands and are relatively large with little overlap. Early wet season areas, however, are all concentrated in the tall grass "valley" regions and are relatively small with a lot of overlap. Large aggregations of elephants of "clan gatherings" only occur during the early wet season. Long communal feeding periods of the units belonging to a kin group also appear to fully depend on the abundance of food. On a seasonal basis, the density of elephants increases with food availability. Hence, during the early wet season, the degree of relationship between any two members of a group of elephants occupying a certain area appears to be low as compared to the dry season or low food availability situation. Under these circumstances, elephants that carry the non-damaging trait do not in the long run profit from the side-effect of this behaviour. The situation of the Namibia desert elephants, however, is rather different: minimal food availability most likely results in (1) low reproductive rate (Jachman, 1986), (2) high mortality rate, (3) low density, (4) very large activity areas, (5) limited overlap of activity areas and hence (6) high degree of kinship between elephants occupying a certain area and a limited time period that elephants spend with non-kin. These factors combined present an ideal situation for kin selection to facilitate the penetration of a "minimal damaging trait".

We could thus describe the relevant parameter as being the mean degree of kinship per elephant per time unit per area unit.

I agree, however, that "maladapted" is not a suitable term for elephants damaging woodlands. Maybe "adapted" should be sufficient to describe the Namibia desert elephants.

REFERENCES

BELL, R.H.V. (1985) Elephants and Woodlands – a reply. *Pachyderm*, No. 5:17-18.

DOUGALL, H.W., DRYSDALE, V.M. and GLOVER, P.E. (1964).

The chemical composition of Kenya browse and pasture herbage. *East African Wildlife Journal*, 2: 86-121.

JACHMANN, H. (1983a). The Ecology of the Kasungu Elephant. Ph.D. thesis University of Groningen.

JACHMANN, H. (1983b). Spatial organisation of the Kasungu elephant. *Bijdragen tot de Dierkunde*, 53 (2): 179-186.

JACHMANN, H. and BELL, R.H.V. (1984). Why do elephants destroy woodland? *AERSG Newsletter*, No. 3: 9-10.

JACHMANN, H. and BELL, R.H.V. (1985). Utilization by elephants of the *Brachystegia* woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*, 23: 245-258.

JACHMANN, H. (1986). Notes on the population dynamics of the Kasungu elephants. *African Journal of Ecology*, 24: 215-226.

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