programmes, and animals killed illegally. Allowances are made for surplus stocks and confiscations, and the quota is separated into amounts which will enter the international trade, amounts which will be used by domestic carving industries and tusks which will be exported as sporting trophies.

For the system to work, both international and internal administrative procedures need to be put in place. Of these, perhaps the internal issues are the more critical since it is only in this area that illegal hunting can be contained and the internal carving industries controlled.

The recommendations from the report together with proposals from the CITES Secretariat were discussed at the 5th Meeting of the Parties to CITES in Buenos Aires in April 1985. A resolution proposing the introduction of the quota system was adopted by the meeting with no dissenting votes.

The key aspects of the new system are as follows:
1. Ivory producing countries will set a quota of tusks which they expect to export in 1986.
2. All present stocks of ivory held by both producer and non–pro-

ducer countries will be registered before the end of 1986.
3. An Ivory Unit will be established within the CITES Secretariat which will maintain a data bank of the registration numbers of all tusks in trade, or likely to enter' the trade.
4. A set of referral procedures will be initiated whereby no shipment is cleared by an importing country until the CITES Management Authority in the exporting country has confirmed the authenticity of the export with the corresponding Management Authority in the importing country. Copies of all export documents will be sent to the CITES Ivory Unit to enable them to monitor quotas and assist in the referral procedure.

The new system should result in improvements, certainly in the ivory traffic between Party States. Hopefully the process of quota setting will focus the attention of the wildlife agencies in producer countries on improving the management of elephant populations and critically identifying the sources of ivory entering the international trade. If all Party States co-operate and the CITES Ivory Unit is successful, the possibility exists of having a daily knowledge of the location of all tusks in legal trade – which would be a major development.

Letters to the Editor

Elephants and Woodland –A Reply

It was a novel experience for me to be lectured by Lindsay and Olivier on my philosophical bias against dynamic change in ecosystem structure (are there other kinds of change?) and about the differences between ruminant and non-ruminant feeding strategies. While I admit that the paper by Jachmann and myself could have been better expressed, I would like to argue the following points:

According to Maglio (1973) the modern African elephant, **Loxodonta africana**, is relatively primitive in its browsing dentition, and evidently remained a forest or forest-margin species until the demise of the grazing **Elephas recki** which occupied the East African savannas until about 35 000 years b.p. On the question of whether the elephant is primarily a grazer when circumstances allow, I am aware of Olivier's (1978) work indicating that **Elephas maximus** selects strongly in favour of monocots in an Asian forest environment; nonetheless, grass makes up a small proportion of its diet. Similarly, with **Loxodonta** we have examined the browse-graze ratio by means of carbon isotope ratios in bone, determined by Julie Lee Thorpe at the University of Cape Town. We find that the browse-graze ratio is a function of woodland density and ranges from about 100% browse in closed forests to about 50% browse in open areas such as Tsavo East. We are now looking for samples from primarily grassland habitats, and would be glad of some Amboseli specimens. However nobody appears to argue that elephants perform better on a diet of pure grass than on a diet containing a substantial browse fraction, or disputes that browse is critical as a dry season food reserve. We may therefore eliminate the first branch of the argument, that the reason elephants kill trees is because to do so stimulates grass production (which it does) and thereby enhances elephant food supplies.

We may assume, therefore, that (perhaps excepting permanent marsh conditions) elephants require a diet consisting of at least 50% browse on a year-round basis. Therefore a key factor in determining elephant population performance is the density of available browse, that is, browse about 3m above ground. The question now is: how does use by elephants affect this value?

Tom McShane and I are currently examining the factors that control the probability that a tree will die or coppice as a result of breakage by elephants, at a number of locations in Malawi. The factors we have identified are as follows:

(a) The probability of tree death seems to be higher in certain species

irrespective of other factors. Susceptible genera are **Acacia, Commiphora**, and **Adansonia**, among others. **Brachystegia, Julbernardia, Isoberlinia, Colophospermum**, some combretums, terminalias, and a range of other species characteristic of the moist-oligotrophic savannas have a higher probability of coppicing, although under certain conditions, as with **Brachystegia boehmii** in Sengwa and Chizarira, Zimbabwe, they may be killed.
(b) Climate: The probability of tree death seems to be higher in more arid areas, particularly below about 600 mm per annum.
(c) Soil conditions: The probability of tree death seems to be higher in soils of higher fertility and lower infiltration rates. Since those factors are mutually correlated, it is hard to distinguish the primary determinant. Perhaps both are involved: more fertile soils support higher biomasses of elephant, leading to more intense use of the vegetation; higher infiltration rates allow greater moisture availability to tree roots and hence may allow coppicing more readily, as well, perhaps as allowing heavier investment in chemical defence. However, in "overdrained" sands moisture availability is low; this may account for the tree death in Sengwa-Chizarira.
(d) Tree size and shape: The probability of tree death is greater in very small and very large trees, while in trees from 2-20cm in diameter the probability of coppicing is relatively high. Further, a tree that has been coppiced once has a low probability of death due to further elephant use. Weyerhauser (1982) made the same point concerning survivors of ring barking.
(e) As a result of the last factor, stand history becomes important. Young stands or stands that have been subject to cultivation or previous elephant use are more resilient to elephants then protected mature stands.

The effect of coppicing is to increase the density of available food for elephants for the following reasons:

(i)   Tree biomass production is stimulated during regrowth;
(ii)   Edible biomass is produced within the height range accessible to elephants;
(iii) Regrowth is of higher primary quality, being younger and thinner than mature material; the effect on secondary chemical defences is unknown and subject to dispute;
(iv)   The edible biomass is denser in space, leading to larger amounts per trunkful and hence faster intake;
(v)   The breakage pattern has the above effects preferentially in preferred species (Jachmann 1984).

Under what conditions do trees respond in this way to elephant use? We argue that over most of the range of both the African and Asian elephants (taking a risk with Olivier involved) the coppice response is characteristic of elephant-woodland interactions. First, there can be no doubt that in most areas of plateau miombo, elephants and woodland can exist in a coppice equilibrium. In Kasungu National Park airphotos indicate that an equilibrium of this type has persisted over at least 40 years. What happened before this is hard to say, although the carbon isotope ratio method does provide a possible avenue to examining the history of elephant-woodland interactions since the browse-graze ratio as indicated by bone isotope ratios appears to be a simple function of woodland density, so that an index of tree density could be obtained from archaeological material. Similarly, the miombo margins of the Luangwa valley appear to be in coppice equilibrium with elephants, although elephant densities are no longer stabile as a result of illegal hunting. Some areas of better drained escarpment miombo do not respond in this way, as indicated above, but these make up a small proportion of the central-southern African mesic savannas. Similarly, Tom McShane has detailed data from Parc "W" in Niger indicating that the West African broad-leaved savanna responds by coppice equilibrium. As for the forest areas, I am not aware of any reports of reduction of forest density by elephants, except at its margins in conjunction with fire, as in Uganda. Primary forest, in fact, is a rather poor habitat for elephants, and much of Olivier's (1978) Ph. D. thesis was devoted to proving, very successfully, that secondary forest, modified by cultivation and elephant activity, provides a more suitable habitat with much more edible material within reach. Alan Rodgers reports similar situations in India.

We conclude, therefore, that it is only in certain of the arid eutrophic savannas that the long term effect of elephant use is to reduce browse availability, and even here this outcome is by no means universal. Rick Weyerhauser (1982), for example, has shown that in Manyara National Park the density of **Acacia tortilis** plants has doubled over about 10 years as a result of the removal by elephants of the mature canopy, thus allowing seedling regeneration. Here, the absence of fire may be a key factor.

We now come to the question of whether elephant behaviour towards trees is adaptive or maladaptive. We may define a trait as adaptive if its probability of representation in the next generation is equal to or higher than that in the current generation, as maladaptive if it is lower. We will leave aside the question of whether tree-damaging behaviour is genetically or socially transmitted, since from the point of view of this argument the two are probably equivalent except in rate of change; we will assume that natural selection operates similarly in both cases.

The immediate advantages to the individual elephant of pushing over trees are the short term effect of bringing the edible biomass within reach, and the more speculative social advantages proposed by Hendrichs and Hendrichs (1971) (wrongly attributed by us to Douglas-Hamilton). If the tree coppices or if it is replaced by regeneration, the elephant obtains further advantages, listed above, delayed by 5-15 years but well within its life span, to say nothing of that of its kin group. We may conclude that, in situations where tree damage results in increased food availability due to coppicing or regeneration, tree damaging behaviour is clearly adaptive in both short and long terms. These situations we believe to cover the majority of elephant habitats.

The question remains, then, of whether tree damaging behaviour is maladaptive in those few situations where neither coppicing nor regeneration occur and a period of low browse availability ensues. The morel look around, the morel have trouble in locating good examples of this type, but certainly Tsavo and Murchison Fails have provided evidence of substantial elephant declines resulting from elimination of woodland while Ruaha and Hwange might have done so had it not been for the poaching and culling respectively. Why, in these situations, has tree damaging behaviour persisted? There seem to be a number of alternatives.

Lindsay and Olivier appear to arguing that a non-tree-damaging trait could hot penetrate a normal elephant population because the short term advantages of allowing the individual to feed on the canopy or bark will invariably outweigh the long term disadvantages of reducing the browse supply, that is, they are worried about a group selectionist argument. Against this, I would quote the situation in Namibia where, according to Anthony Hall-Martin, the desert elephants do not damage trees, but feed on them on a sustainable basis, implying that where the long term disadvantages of tree damage are sufficiently strong, a non-tree-damage trait can penetrate the population. In fact the clan system of elephants, with its relatively exclusive use of resources by kin groups, provides rather favourable conditions for the spread of resource-use limitations through kin-selection.

An alternative possibility is that the tree-dam aging trait has not in fact persisted in the localities named. Do we know that it has survived the crash in Tsavo? It would be worth checking. (This alternative implies that the stable limit cycle has not been a regular feature of elephant-woodland interactions, but don't worry, I am one of Caughley's most fervent admirers).

A third possibility is that the surviving elephant populations will capture the regeneration (when it occurs) in a coppice equilibrium, again implying that the pre-Park mature woodlands were a man-induced artefact.

A fourth possibility is that the stable-limit cycle has been a regular feature of the arid-eutrophic savannas but that, following each crash, the affected areas have been recolonised by elephant from surrounding moist-oligotrophic areas, carrying with them the tree-damaging trait.

On the whole, I prefer the last alternative. Is mailadaptive the right word for this situation? Perhaps not, does it matter?

Finally, after all this technical detail, I ask myself what Lindsay and Olivier are **really** worried about. Usually this kind of argument has its roots in some concern about culling. If so, let me once again make my position perfectly clear: The decision as to whether or not to cull is only indirectly related to the technical aspects of the elephant-woodland interaction; it depends on the objective for the area and rests equally on a set of aesthetic decisions (Bell 1983). Neither the compression model nor the stable limit cycle model nor the coppice equilibrium model by itself argues for or against culling. In Kasungu National Park, for example, the master plan calls for maintenance, through elephant culling, of the mature woodland structure with its specialised woodland fauna (sable, roan, hartebeest, etc) of part of the Park, and for no manipulation of the areas already stabilised as coppice equilibrium (Bell 1981).

R.H.V.   Bell, Senior Parks & Wildlife Officer (Research),
Dept. of National Parks and Wildlife,
Malawi.

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