Letters to the Editor

ELEPHANTS AND WOODLANDS—WHAT ARE THE ISSUES?

When we decided to respond to the article on elephant/woodland interactions by Jachmann and Bell (1984), Rob Olivier and I recognized a number of separate issues which we felt deserved comment. We hoped to stimulate discussion, rather than 'lecture" the authors, but because we were limited to a small space for our letters (Lindsay and Olivier, 1984), we were able to deal with only a single point each, and perhaps neither particularly well. Bell's (1985) reply continued the dialogue and answered some of our concerns. However, a few contentious points remained, and this "reply to Bell's reply" discusses more fully the issues we considered important.

Bell (1985) suggested that what we were "really worried about" was the issue of culling. This is accurate in so far as we feel that management interventions, such as culling (and burning, water development, and translocation), have impacts on ecological processes, and should be cautiously applied or avoided for valid reasons. What concerned us about the Jachmann and Bell article was the authors' use of ecological and evolutionary arguments mixed with opinion to support an apparent preference for short term stability (versus "dynamic" fluctuation) in savanna community structure, and for management intervention to preserve a given status quo. This position surprised us, in view of Bell's (1983) earlier commitment to a separation between "aesthetic" opinions and "technical" facts in the decision-making process. The questions posed for scientific study and the application of research results to management may incorporate value judgements, but we agree with Bell in the view that ecologists ought to be philosophically neutral when they discuss the scientific aspects of elephant biology. To do otherwise is to bias the decision-making process from the outset. An ecologist might properly say""Elephants alter woodland to grassland", leaving t to the manager (or to his own manage*r persona*. if he wears two hats) to say "Elephants destroy roan antelope habitat" or "Elephants create wildebeest habitat" and to judge this process as desirable or riot. Similarly, while the term "maladaptation" has an objective, scientific meaning, t can also be subtly persuasive when t addresses our attitudes towards management: can our sympathy for a "maladapted" organism be as great as for its""well-adapted" cousins? Bell's reply clarified the technical and aesthetic issues, and was more generous in its attitude towards ecological change. We find ourselves in closer agreement with this approach.

Technical questions were covered more extensively in the reply than in the original, but further discussion might still prove useful. One of these concerns elephants' dietary requirements. Can we really say that all elephants **need** a diet with a substantial browse fraction, simply because that is what they have been seen to eat in certain places and times? Olivier has suggested that elephants primarily need large quantities of plant material containing digestible energy, with supplements for specific amino acids or minerals if they are not found in the bulk diet. Grass is a good food source for large herbivores because its cell wall is not highly lignified (and is therefore fairly fermentable) and toxin levels are generally low. Woody browse may have larger amounts of soluble nutrients in its leaves and bark, but also contains more lignin and secondary compounds. Greater feeding selectivity, high turnover rates, and/or detoxification mechanisms may be needed by herbivores ingesting large amounts of browse. The relative abundance of grass v browse in a habitat will influence its inclusion in the diet. It seems that where and when grass is abundant, t supplies much of the dietary bulk for elephants. In dry seasons, or in habitats where woody vegetation is dense and grass sparse, browse will **necessarily** form a larger part of the total diet. In certain Asian forests, palm leaves are a major food of elephants technically palm leaves might be called "browse" since they come from trees, but as monocots, they more closely resemble grass in their chemical structure. Where marshes are found, as in Amboseli, swamp sedges are prominent even in dry season diets. The categorization of elephants as primarily grazers or browsers is clearly an oversimplification. They are generalist""mixed feeders" with large absolute requirements for nutrients (because of their size) and they make opportunisitic use of locally available resources. Indeed, nobody disputes that browse is important as a seasonally or regionally abundant food source; equally, few should disagree that grasses (or other monocots) are also important and are actively chosen when available.

A second technical issue concerns the development of equilibria in interactions between elephants and woody plant communities. Bell's research into the factors favouring coppice equilibrium demonstrates that some relatively unpalatable tree species, under certain environmental conditions, can grow back after elephant feeding and produce stable equilibrium communities. Absence of elephants appears to result in a community dominated by different woody species. The effects of herbivory on plant community structure have also been observed in grassland communities under the influence of grazing ––is this process qualitatively different from the elephant/tree interaction? There may be greater potential for instability in arid eutrophic systems, because higher nutrient density in woody plants may promote higher herbivore biomass and lower rainfall can limit compensatory plant growth, as Bell (1984) noted. Greater yearly variation in arid zone plant production and time lags in elephant and tree population responses could increase the instability, contributing to cyclic or irregular fluctuations. Bell (1985) also suggests how other ecological factors, such as fire, could contribute to the dynamics of arid zone communities. Our understanding of the factors affecting persistence and stability in elephant/woodland systems is developing slowly but steadily as more exstensive, longer term data on both plants and elephants accumulate. However, the Manyara example shows that "damaged" woodlands can regenerate under favourable conditions ––similar regrowth appears to be underway now in parts of Tsavo. There seems no reason to assume that all fluctuations must be catastrophic or irreversible, or that stability is never possible in arid eutrophic ecosystems.

In view of the foregoing, the suggestion that stable equilibria must occur by "husbandry" of woodlands by elephants seems unnecessarily complicated. It shares the theoretical difficulties of resource husbandy models, which require that discounting of short term benefits against longer term advantage be favoured by natural selection. In the case of elephants' use of trees, two hypothetical traits, tree damaging (TD) and non-damaging (ND) must be defined. Given the same local conditions, we will assume that both traits satisfy nutrient requirements in diets with the same grass/browse ratio; but TD animals break most of the trees they feed on while NDs do not (R. Bell, pers. comm.). ND individuals should take care not to damage trees, if necessary by visiting a greater number of trees over a larger area, and feeding less intensively on each single one. A "true N D" should do this even when ts immediate foraging needs (and perhaps short term survival chances) would be better served by feeding intensively on palatable, localized trees. Additionally TDs might be expected to make an extra effort to damage trees, not just when necessary to get a food source such as twig tips, leaves, or fruits, but simply to stimulate coppicing for future feeding. According to the husbandry model, TD should be selected for in moist oligothrophic areas where damage leads to coppicing, while N D should be favoured in arid eutrophic areas where trees are apparently more likely to die when broken or debarked (Bell, 1985)..

It remains difficult to see how such traits could spread through populations by natural selection. In moist oligotrophic woodlands, if a TD elephant coppices a tree and an ND neighbour does not, ND and its offspring will still get the long term benefit from increased browse abundance. On the other hand, in arid eutrophic areas, if TD kills a tree, its ND neighbour will also suffer. Assuming the energy costs of damaging or avoiding damaging trees are small or balance out, the TD and N D traits would not confer any relative advantage to their possessors over individuals carrying the opposite traits. It also seems that "cheaters" seeking short term gains could easily invade and disrupt the system. For this type of resource husbandry to work, individuals or closely bonded social groups must have long term exclusive control over their foraging ranges. Does resource monpolisation occur in elephants? Details of elephant social organisation are still under study in Addo, Amboseli, Hwange, and elsewhere, and any conclusions must be tentative. From the work done thus far, t appears that while putative elephant "clans" may have "relatively" exclusive use of the core area of a shared range, the number of individuals included may be large (over 100) and social relationships beyond the level of family unit may be fairly diffuse. Social bonding in mammals is often based on kinship, and elephants in family units maybe as closely related as mother-offspring pairs or full sibs (r = 1/2). However, kin relations may more often be half-sibs (1/4), half-aunts (1/8), half-cousins (1/16), or more distant. Clan areas appear to include a number of overlapping family unit ranges, making average relatedness lower still. Reciprocal relationships between non-kin have been found in some primate groups, but such groups with exclusive home ranges are generally sedentary and small in size. The inclusion of bulls further complicates the picture. There is often some overlap of bull areas with those of presumably unrelated females; among bulls sharing the same area, the relatedness of most individuals may be lower than within female clans. With our present understanding, it appears that the level of control over plant resources possible under the social system of elephants would be insufficient to allow the development of husbandry traits by individual, kin, or non-kin group selection.

It may, therefore, be inappropriate to describe elephants as maladapted when they do not appear to husband tree populations (or well-adapted when they do). It seems more likely that neither the TD or ND extremes are accurate descriptions of elephant feeding behaviour. Instead, elephants appear to feed on the parts of woody plants which they need to satisfy immediate nutritional needs. Damage may thus be an inevitable cosequence of efficient foraging in the short term. However, future studies of elephant feeding behaviour could examine more closely the context and relative inicidence of damage to woody plants, to further examine this question.

Despite these difficulties, many of the ideas proposed by Bell, especially in his reply letter, are stimulating amid suggest some priorities for research. For me, an important additional point was the policy statement recommending no culling in part of the Kasungu system. Although this recommendation was made for practical reasons — a massive culling programme would be required to reverse the elephant impact at this point, and further vegetation change appears unlikely (R. Bell, pers. comm.) — t also represents an opportunity to test the coppice equilibrium hypothesis. While such an experimental approach may be deemed undesirable for human social reasons in many areas, t is valuable whenever possible to gain knowledge about the biological principles underlying elephant/tree interactions and management options.

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Comment by R. du Toit (Co-Editor)

Sikes (1968) found that elephant hiving in lowland East African parks that were comprised largely of degraded scrubland or grassland had a high incidence of arterial diseases (median sclerosis and atheroma) and many had abnormally-shaped hearts, while elephant in montane forest areas were virtually free of these problems. This study did not establish whether these diseases were primarily due to dietary deficiencies, or to postulated stress factors (such as overpopulation, frustration of migratory habit, and excessive exposure to sunlight). McCullagh amid Lewis (1967) also found arterial lesions in most elephant sampled during population reduction exercises in Murchison Falls National Park amid Tsavo National Park, and ascribed the lesions to a lack of dietary lipid. McCullagh (1973) suggested that excessive tree damage by elephant may be a natural response to an inadequate fatty acid intake, since trees such as baobabs and **Terminalia** species which were particularly sought after by elephant in Tsavo and Murchison Falls have relatively high concentrations of linoleic acid (which was found to be particularly deficient in the elephants' diets).

White and Brown (1978) sampled elephant in a grassland habitat of the Kabalega National Park, which had an apparent overpopulation of elephant; they found a number of animals that showed polycythaemia (not found in elephant in the forested Ruwenzori National Park) and postulated that this was related to cardiovascular disease. Cmelik and Ley (1977) found that elephant in the Wankie (Hwange) National Park— where woody browse is readily available—— had relatively high levels of chohesteryl linoheate, even in the dry season, indicating that they must be receiving sufficient linoleic acid in their diet.

In view of these observations, t is surprising that Keith Lindsay asks: "Can we really say that all elephants NEED a diet with a substantial browse fraction, simply because that is what they have been seen to eat in certain places and times?" Richard Bell (pens. comm.) says that knowledge of the possible relationship between the incidence of arterial disease in elephant amid the proportion of woody browse in their diets is taken for granted in his letters. The above review of relevant literature is incomplete, and t would be useful if someone with a sound knowledge of these physiological aspects contributed some comments to the debate on elephant and woodlands.

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ELEPHANT TAXONOMY

Colin Groves and Peter Grubb are attempting a taxonomic revision of hiving elephants, using mainly characters of the skull, and would appreciate information from anyone who has measured even parts of an elephant skull of KNOWN LOCALITY (and, preferably, known sex and known age — dental eruption stage). Required measurements are given below; the figures indicate the position in which each measurement is, in our experience, most conveniently taken.

So far, we fiave between us nieasured all skulls in all the major collections of Europe and the United States (and in many minor collections too). Some very preliminary observations are as follows.

(a) Among African elephants, **cyclotis** is very distinct indeed from ordinary **africana**. Among the differences are the shorter, broader rostrum, the lesser degree of mastoid inflation, the longer mandibular syniphysis, the smaller teeth, and the fact that measurements (3) and (4) are usually identical (whereas number (3) is always greater, by several centimetres, in ordinary africana). We have, however, indications from a few skulls in the Brussels Museum that interbreeding occurs in the Virunga National Park, Zaire; and we would hike to hear from anybody who has evidence that the two interbreed anywhere else, or conversely approach each other without apparently interbreeding.

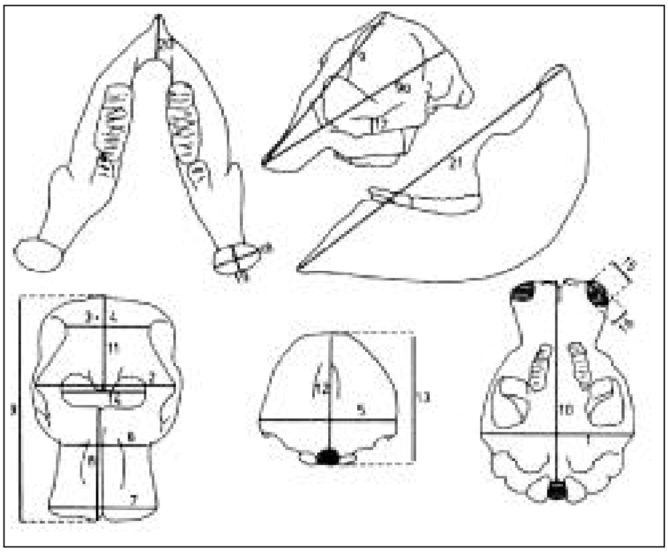
(b) Among Asian elephants, there seem to be two basic divisions: a "mainland" group (also in Sri Lanka), and a smaller "insular" group (also Malaya). The degree and amount of depigmentation seems to differentiate these two groups. Within the first group, t seems to us in possible so far to distinguish a Sri Lankan race, unless at the same time the big Mahavili elephants (vilaliya) are distinguished from the smaller mountain forest or general Sri Lankan form. Within the second group, the elephants of Borneo do seem distinguishable from those of Sumatra and Malaya: we incline to think they are indigenous, not introduced.

REQUIRED SKULL MEASUREMENTS:

1. Bizygomatic breadth;
2. Width across postorbital processes;
3. Width across postorbital constriction (least);
4. Width between temporal lines (least); this may be the same as (3) or t may be somewhat less;
5. Greatest breadth of occiput;
6. Least width of rostrum;
7. Greatest width of rostrum;
8. Length of rostrum;
9. Greatest skull length in midline;

9.a Greatest skull length, if occipital inflation is great enough to make a measurement taken from occipital surface exceed (9);

10. Basal length;
11. Occipitonasal length;
12. Occipital height, from opisthion;
13. Occipital height. fronm basion;
14. Width of external naris, taken between the ridges bounding t laterally;
15. Width of incisor alveolus: mesiodistal;
16. Width of incisor alveolus: buccoligual;
17. Least depth of zygoniatic arch;



18. Greatest diameter of mandibular condyle;
19. Diameter of condyle at right angles to (18);
20. Length of mandibular syniphysis;

AND

Breadths of all teeth present, arid state of eruption;
Lengths of all teeth present —if erupting, then length that is in wear; if being shied, then length that still remains;
Number of lamellae (a) visible and (b) in wear on each tooth;
State of following sutures: (a) internasal, (b) bordering naris, (c) naxillo-premaxillary;
Length of humerus; radius; femur; tibia;
Numbers of vertebrae in each spinal segment;
Any external measurements available.

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CITES DEVELOPMENTS

Singapore has been a trade centre for rhino horn in eastern Asia, since the country did riot adopt CITES trade restrictions concurrently with other trading countries. However, as of 24 October 1986, the import and export of rhino horn has been prohibited by the Singapore Government and thus there is hope for some reduction in the trade in Eastern Asia.

An extremely significant development is the agreement by the Government of Burundi to enforce C ITES procedures for the control of trade in ivory. As of 1 September 1986 all imports and re-exports of ivory from Burundi have become subject to complete CIT ES controls. The Burundi Government has registered stocks of raw ivory totalling 89 502 kg.

Senegal has adopted new legislation on ivory trade, which makes the export of raw ivory illegal, except in the case of illegal hunting trophies.