

Why do elephants damage savanna trees?

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ELEPHANTS DAMAGE AND KILL TREES. THIS behaviour often appears to be excessive because their immediate, subsequent consumption of edible parts of these trees is often negligible. Some trees later resprout after snapping and toppling by elephants and thus produce forage at the animals' preferred feeding-height. We argue that this and other 'farming' hypotheses are group-selectionist and are thus not evolutionarily stable strategies. We suggest that excessive damage to trees is more likely to be due to social or sexual factors. More behavioural analyses and experiments are needed to understand this phenomenon and its implications for conservation.

Introduction

Elephants are or were responsible for toppling large knobthorn trees (*Acacia nigrescens*), snapping marula (*Sclerocarya birrea*) and mopane (*Colophospermum mopane*) trees as well as bark-stripping baobabs (*Adansonia digitata*) in many parts of the African savannas. This level of damage appears excessive because only a few leaves or pieces of bark or roots are subsequently eaten,¹ and because persistent elephant damage can lead to the death over large areas^{2,3} of trees that include the preferred fodder species of elephants. For example, marula, baobab, knobthorn and certain succulents (such as *Aloe* species), all highly palatable species for elephants, have variously been decimated in some parts of the Kruger National Park, South Africa.⁴ There is an extensive literature documenting these and other aspects of elephant foraging and its implications for conservation and biodiversity (see recent bibliography at www.elephant.chebucto.net). However, the evolutionary understanding, as opposed to the ecological consequences, of why elephants inflict this level of damage is lacking. Thus, there is no synthesis of this topic in the reviews of Owen-Smith⁵ or Whyte *et al.*⁴ To promote this understanding, our main aims here are to 1) review and collate current hypotheses of why elephants snap and topple trees and 2) suggest that the

presently favoured 'farming' hypotheses cannot explain the evolution of this elephant behaviour. We conclude with speculations on 3) social/sexual hypotheses as possible explanations, and propose directions for future research.

Costs and benefits of snapping and toppling trees

The snapping and toppling of trees has an immediate cost to the individual elephant involved in terms of time and energy. There may also be delayed costs and benefits. For example, since individual elephants are long-lived and have a long reproductive phase, those individuals involved in snapping and toppling may also experience the fitness costs of loss of future browse due to the decline of palatable woody species. This is because the rapid elimination of weak resprouting *Acacia* species in a particular savanna may occur within the reproductive period of the individuals involved in damaging the trees. The fact of these short- and long-term costs suggests that evolutionary reasons should be found for this behaviour. The hypotheses (listed as H1–H6 below) as to why elephants indulge in tree snapping and toppling can essentially be grouped into three: 1) a form of adaptive 'farming', or 2) due to sexual/social factors, or 3) as being non-adaptive.

Elephant farming hypotheses (H1–H2)

By 'farming' we mean the short-term costly attempt at long-term (that is, delayed benefits) modification of the structure or composition of plant communities for the benefit of the individual elephant (and/or its descendants) concerned. This non-altruistic behaviour implies both considerable spatial and temporal memory, to ensure that the destructive animal predominantly reaps the rewards.

The presently favoured hypothesis argues that damaged trees may recover by subsequently resprouting and thus the snapping and toppling is effective because it lowers the browse height (H1) to one preferred by elephants.^{1,6,7} Excessive elephant damage is therefore seen as a form of farming in which tree canopies are merely lowered and this

action causes no decline in the tree population. Smallie and O'Connor⁸ suggested that the creation of hedges in mopane is the benefit to elephants for snapping and toppling. Styles and Skinner⁹ go further and suggest that the ability of mopane to form hedges in response to tree damage means that apparently heavily impacted areas do not therefore require any specific conservation intervention.

The long time delay between the snapping and toppling event and the pay-off (foraging on replacement palatable plants or sprouts) renders it unlikely that there are selfish benefits to the elephant responsible. Also, because individual elephants move over large areas,⁷ rather than defend territories and thus hedges they have created, the individual responsible for the snapping and toppling (or their genetic offspring because the damage is normally inflicted by males) cannot ensure exclusive future foraging benefits from hedges it has created. We suggest that H1 also implies an unlikely degree of spatial and temporal memory and territoriality by elephants. Importantly, it cannot explain why or how cheaters (elephants that do not indulge in snapping and toppling, which include most females and juveniles) would be disadvantaged, since they too would have access to hedges created by males.

A further criticism of H1 is that snapping and toppling leads to local decimation of certain forage tree species, especially of non-hedging *Acacia* species and tree succulents¹⁰ and not just the lowering of canopy height. This kind of tree damage can lead to death rather than the production of 'browsing lawns'. Also, since the damage may include non-preferred tree species,¹ which would at least give shade, it suggests that the reason elephants damage trees is not always for future foraging on hedges.

Long-term foraging gains, not involving resprouting, could accrue to elephants involved in snapping and toppling if any unpalatable trees killed were replaced by palatable species, within the fertile period of the elephant concerned and if this individual obtained largely exclusive benefits of any new browse species. We consider this as generally unlikely because recruitment dynamics (from seed to 'browsable' dimensions) takes several years in savannas, because unpalatable species may replace palatables⁵ and because elephants may actually prevent recruitment of palatable species.³

Snapping and toppling may occur because elephants prefer grazing (H2) and thus convert, or 'farm', trees into

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grasses, not hedges. A criticism of this is that although elephants are predominantly grazers, they choose to consume considerable browse,¹⁷ especially in areas with grass die-back in the dry season. Therefore, the decimation of browse plant species is not necessarily adaptive. The H2 argument, like H1, suffers from being group-selectionist. It can neither explain how the individual elephant involved in snapping and toppling trees would access the direct and exclusive benefits to the grass nor how cheaters would be excluded from it. In short, it is unlikely that any farming hypothesis (H1 and H2) for this kind of damage is an evolutionarily stable strategy.¹⁰

Non-adaptive hypotheses (H3–H5)

Snapping and toppling trees may be merely a consequence of over-robust feeding (H3), especially by larger male elephants. This is unlikely, however, because there are many examples of how selectively and delicately elephants can feed. An illustration of this is the observation that elephants have removed almost all mistletoes, including the mimetic species, within the elephant enclosure in the Addo Elephant Park.¹¹ This implies remarkable powers of selective feeding.

Stokke and du Toit¹² noted a greater preference for coarse browse by males than females. This would not explain the need for males to fell trees, however, because they do not feed on large stems. It also suggests that females and juveniles would benefit more from the hedging response of plants than the males that inflict the damage on trees, because females prefer less coarse browse and, being shorter, cannot reach into the taller canopies.

Jachmann and Bell¹³ postulated that today's East African savanna elephants are forest elephants displaced from central Africa (now accepted as *Loxodonta cyclotis*) or interbred hybrids that have recently taken over the savannas as a result of excessive hunting for the ivory of savanna elephants. They suggest that widespread tree snapping and toppling in East Africa is a recent behaviour of the present savanna elephants (H4), and that it is a non-adaptive, instinctive behaviour of forest elephants. This hypothesis is incorrect genetically; forest elephants are distinct from all savanna elephants.¹⁴ Also, this would not explain why forest elephants damage trees, nor why males predominate in this behaviour.

Russell,¹⁵ Guy¹ and others have considered tree destruction by elephants to be a deviant behaviour (H5) brought about by

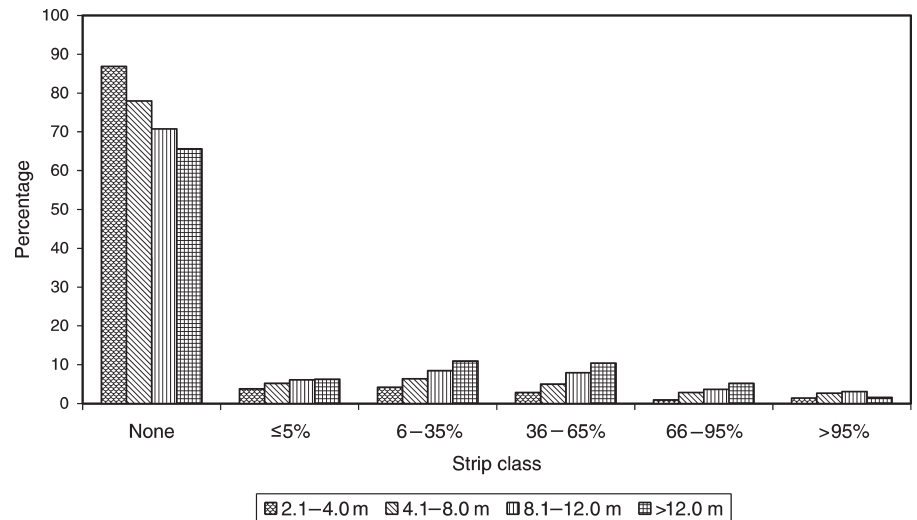


Fig. 1. Percentage bark stripping per height class in *Acacia* species in Hluhluwe–Umfolzi Nature Reserve. The study sample consisted of 359 plots, each measuring 50 m × 50 m, with 9320 individual stems. Percentage refers to the proportion of the circumference affected.

recent disturbances to the animals, for example by shooting or their being fenced-in. Furthermore, they argue that it could be a normal (= adaptive) behaviour in once free-ranging animals but that snapping and toppling trees is now more conspicuous because elephants are compressed into smaller conserved areas. This could be tested by determining whether the extent of this kind of tree damage varies with elephant densities. However, it would not explain why they snap and topple trees in their previously unrestricted range.

Sexual or social hypotheses (H6–H7)

Here we consider whether elephants topple trees for selfish benefits, related to genetic consequences of male–male or male–female interactions. Croze,¹⁶ Guy¹ and others have noted that males cause most of the damage and, on this basis, Guy¹ suggested it was a social display phenomenon (H6) and not a feeding necessity. Hendrichs¹⁷ suggested that snapping and toppling could influence bachelor hierarchies. Another possibility is that it would influence the males' access to females. We suggest that a male–male or a male–female display hypothesis is unlikely because solitary males inflict the damage (personal observation), as do non-dominant bulls^{1,17} and also matriarchs.¹ Moreover, because the visual sense of elephants is poor and the bulls' home ranges overlap,^{18,19} it is not clear how the display would be affected because it would require others males, or females, to be able to identify the perpetrator.

We suggest that the short-term selfish gain to individuals inflicting tree damage is that it is a form of gymnastic training and 'confidence building' (H7) related to

contests and dominance (e.g. Estes²⁰), especially amongst males. This hypothesis leads to the prediction that elephants will push over experimental metal poles that yield no forage, indicating that this behaviour should not be seen only as a foraging tactic. Elephants push over powerline and signage poles in Addo Elephant National Park (J. Adendorf, pers. comm.) and Kariega Game Reserve (M. Fowler, pers. comm.).

Some aspects of bark removal are similar to toppling trees, in that it can be too excessive to be a feeding necessity and that it also leads to the death of woody plants. Possibly bark stripping can also be explained as being for social/sexual reasons, such as a training exercise for contests with tusks.²⁰ In Hluhluwe–Umfolzi Nature Reserve we noted patterns of bark removal in *Acacia* species in 359 quarter-hectare plots spread across the reserve. Elephants stripped the bark of trees both large and small. However, the animals are dexterous enough to remove only a very small amount of the bark from even the smaller stem (Fig. 1). If bark removal was a 'farming' activity intended to replace woody species with grasses, we would expect greater levels of ring-barking (that is, more than 95% removal of the circumference) than is apparent from the figure. If bark-stripping was a feeding activity, we would expect that mainly small amounts would be removed. We observed that elephants do not eat much of the larger strips they separate from the main stem and in many cases this bark merely remains partially attached at the base of the tree. In the 359 plots at Hluhluwe, we noted that elephants stripped the bark of 25% of milkwood (*Sideroxylon inerme*) and 6.4%

of tambothi (*Spirostachys africana*) trees, both non-fodder species for the animals. This suggests that bark-stripping is not a feeding response by elephants and is another poorly understood activity that can lead to the loss of woody plants either directly or indirectly via subsequent fire or insect damage.

Future research

Understanding why elephants indulge in tree snapping and toppling will require further observations and experiments. The typical *post hoc* observational approach (such as by surveys of past elephant damage) has limitations; for example, it does not indicate failed attempts by elephants to snap and topple trees. Do elephants preferentially attempt to select trees that are easily toppled (for instance, those with weak or brittle wood, or shallow root systems), rather than more resistant species? If so, this could argue for the sexual-display hypothesis. Positive selection of non-fodder (such as poisonous) trees for damage would also argue against the hedging hypothesis. There is evidence that elephants attempt to go for larger trees than they are capable of toppling.¹ These trees would offer good training opportunities but poor 'confidence building' or display opportunities because they are less likely to be toppled. Large trees should be avoided by an optimally foraging elephant. If snapping and toppling regularly occurs as an activity of solitary males, it would favour a training hypothesis over a display hypothesis. Do males or females respond to the sound of a tree being toppled? Is this activity associated with males in musth?

Bark-stripping also needs more study. The gender of elephants involved in bark-stripping has not apparently been studied and it will be important to note differences in amounts of bark stripped by bulls versus cows. The sexual hypothesis predicts that males will predominate in excessive bark-stripping, as they do with tree snapping and toppling. This is not because tusks are disproportionately bigger in males (a large tusk is not needed to peel-off significant amounts of bark), but because males will benefit from increased tusk dexterity in interactions with other males. Do elephants target tree species for bark removal on the basis that are more prone to stripping (for example, do they favour thick-barked trees)? Does bark stripping have a social connotation

(is the activity pursued by solitary individuals or those in herds) or sexual aspects (is it more likely performed by males in musth)? Are non-palatable species targeted for bark-stripping?

The geography of tree snapping and toppling needs investigation. Viljoen and Bothma²¹ suggested that the desert elephants of the Kaokoveld have no detrimental effect on the vegetation they encounter. We find this proposition unlikely because it is group-selectionist and unsupported by their data (for example, they had no control site). There would be no benefit for any individual elephant to moderate its feeding behaviour, even in a supposedly fragile environment. Viljoen²² went to the extreme by suggesting that the self-controlled feeding methods of desert elephants inflict only moderate browsing damage and that this may actually be beneficial to desert plants by reducing their transpirational leaf area. Besides being highly unlikely, it also implies a group-selectionist perspective. We predict that geographical differences in their damage to trees will not be due to altruism on the part of elephants but result from other factors such as tree size, strength and rooting-depth.

Recently, Linklater²³ bemoaned the lack of integration of proximate and evolutionary approaches in conservation biology. Tree snapping and toppling by elephants may be a case in point. An understanding of why individual elephants indulge in this activity may inform conservation solutions for areas where elephant damage is excessive. For example, H6 predicts that high levels of this damage occur as a result of disrupted elephant hierarchies (as a consequence, for instance, of trophy hunting, introductions or culling) and that culling family groups maybe relatively less useful than culling bulls. If true, it implies that the maintenance of hierarchies by conservation authorities may minimize damage to trees, just as there were fewer elephant attacks on rhinos after dominant males were re-introduced to suppress prolonged musth in adolescent males.²⁴

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