

Wire netting reduces African elephant (*Loxodonta africana*) impact to selected trees in South Africa



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African elephants (*Loxodonta africana*) are ecosystem engineers in that they substantially alter the environment through their unique foraging and feeding habits. At high densities, elephants potentially have negative impacts on the environment, specifically for large trees. Because of this, recent increases of elephants in the Associated Private Nature Reserves (APNR) on the western boundary of the Kruger National Park (KNP), South Africa, have caused concern regarding the survival of several tree species. Our objective was to assess the effectiveness of wrapping protective wire netting around the trunk of the tree for preventing and reducing bark stripping, branch breaking, and felling by elephants. We assessed 2668 trees – 1352 *Sclerocarya birrea* (marula), 857 *Acacia nigrescens* (knobthorn), and 459 *Lannea schweinfurthii* (false marula) – for elephant impact in the APNR, 1387 (52%) of which had previously been wrapped in protective wire netting (789, 548 and 50, respectively). Wire netting was effective in reducing the severity of bark stripping and the relative proportion of trees that were bark stripped. In addition, wire netting had an effect on the level of impact, with a higher relative frequency of wire-net-protected trees found in lower impact categories compared with unprotected trees. Since tree mortality has been attributed to high levels of elephant impact, the use of wire netting could serve to maintain individual trees or populations particularly vulnerable to elephant impact in areas with locally high densities of elephants.

Conservation implications: Since wire netting is a relatively low cost and ecologically unobtrusive strategy, it could be used to reduce elephant impact in problem areas. This method focuses on protecting trees rather than some other strategies such as environmental manipulation, translocation, contraceptives, and culling that instead focus on reducing elephant numbers.

Introduction

Elephants are allogenic ecosystem engineers (Jones, Lawton & Shachak 1994) in that they substantially modify the environment through their unique foraging and feeding habits (Laws 1970). In areas where elephants are confined by fences and human settlements, their population density can increase locally, leading to extensive modification of habitat that can potentially have negative consequences on ecosystem processes and other organisms (Dublin & Hoare 2004). For example, Vogel *et al.* (2014) proposed that elephants could affect vulture and raptor nesting sites by allowing opportunities for insect and fungal attack after bark stripping, and therefore reducing tree survival. Guldemon and Van Aarde (2008) list a number of studies where high densities of elephants were found to negatively impact woody vegetation, but caution that the findings are site-specific and dependent upon environmental conditions. Within the Kruger National Park (KNP), managing elephants in relation to vegetation changes has been a longstanding topic of concern (Ferreira *et al.* 2011; Gaylard & Ferreira 2011; Young, Ferreira & Van Aarde 2009). Large trees are of particular concern, because elephants are one of only a few biotic forces that can directly and rapidly modify this key feature of the savanna landscape (Asner *et al.* 2015; Laws 1970; Morrison, Holdo & Anderson 2015). Large trees play an important role in the biogeochemical cycles of the savanna as well as indirectly affect the distribution of numerous sympatric species that use the trees for refuge, shade, nesting, food, and other activities (Bernhard-Reversat 1982; Nasser, McBrayer & Schulte 2010; Vogel *et al.* 2014).

Elephants can affect trees in a variety of ways, including bark stripping, breaking branches, breaking the main stem, or uprooting the entire tree (Boundja & Midgley 2010; Henley 2013). Bark stripping and branch breaking expose trees to insect attack and greater damage from fire, both of which may

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result in tree mortality (Helm *et al.* 2011; Vogel *et al.* 2014). Trees are particularly vulnerable to a type of bark stripping known as ringbarking, where the bark is removed around the entire circumference of the tree (Helm *et al.* 2011; Ihwagi *et al.* 2009). Tree species differ in their vulnerability to impact because elephants selectively browse for particular species or because of certain characteristics that could predispose a tree to extirpation (Boundja & Midgley 2010; O'Connor, Goodman & Clegg 2007). Boundja and Midgley (2010), for example, found that elephants preferred larger trees and therefore targeted larger, less abundant species in Hluhluwe-Imfolozi Park, South Africa. Elephants are also known to favour trees with certain chemical composition, choosing to browse trees with high levels of leaf nutrients such as calcium, magnesium, potassium, and protein (Holdo 2003). Although extensive branch breaking and felling can alter the form of a tree, species that readily coppice after such events can survive and continue to grow if their roots remain intact (Eckhardt, Van Wilgen & Biggs 2000; Henley 2013; Ihwagi *et al.* 2009). However, the continuing loss of habitat for elephants because of expanding human populations and/or fencing compresses their range and confines them to certain areas for unnaturally long periods of time. This often results in continuous and persistent impact that alone or in combination with other factors such as fire or insect attack leads to increased risk of tree mortality (Boundja & Midgley 2010; Mapaure & Moe 2009; Van Aarde, Jackson & Ferreira 2006).

Many conservation management plans focus on reducing elephant numbers in order to reduce impact, often assuming a direct linear relationship between the two (Van Aarde *et al.* 2006). However, some research has suggested this is not the case and that other factors may be involved (Young *et al.* 2009). Environmental manipulation, translocation, contraceptives, and culling have all been suggested and used at various times in South Africa's history to reduce elephant densities (Du Toit, Rogers & Biggs 2003; Van Schalkwyk 2008). Alternatively, management could focus on protecting the trees themselves. Wrapping wire netting around the trunk of a tree is one such technique that was first employed in Kenya (Gordon 2003). If wire netting decreases elephant impact in other areas and over the long term, it could serve as a cost-effective and ecologically valuable solution to continuous elephant activity in confined areas. The aim would not be to protect all trees of a certain species and thereby potentially increase the impact on other, unprotected species. Instead, the technique can be used to protect individual trees or areas of specific species to ensure there will always be enough mature specimens to populate the surrounding landscape with their seeds.

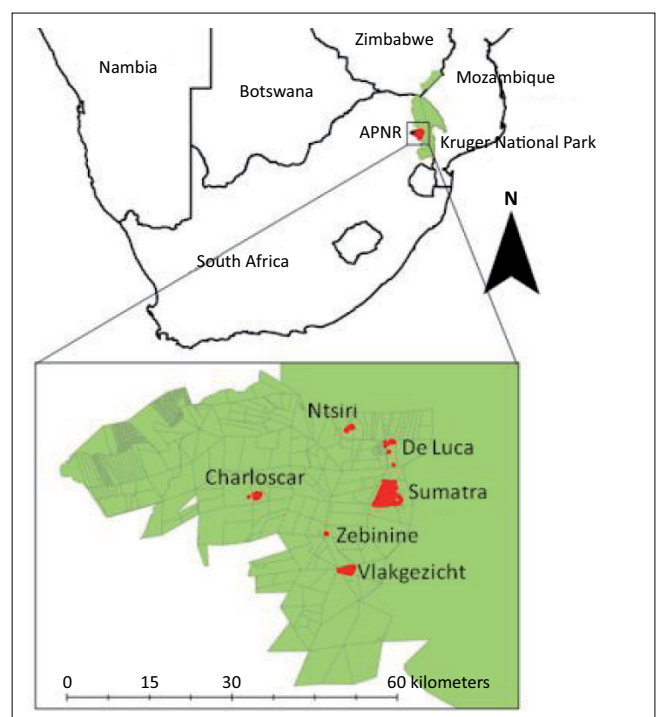
The objective of this study was to assess the effectiveness of wire netting in reducing elephant impact to three relatively abundant, iconic, larger (> 5 m) tree species, namely *Sclerocarya birrea*, *Acacia nigrescens*, and *Lannea schweinfurthii*. Wire netting is designed to reduce bark stripping, but we examined all forms of impact by elephants to determine if there was a relationship between wire netting and elephant impact in general.

Methods and materials

Study site

This study was conducted in the Associated Private Nature Reserves (APNR), an area of over 1800 km² adjacent to KNP, South Africa (Figure 1). Together, the APNR and KNP encompass an area of more than 20 000 km² of conserved land and sustain numerous valuable animal and plant species (Gertenbach 1983; Joubert 1996). The APNR includes Balule, Klaserie, Timbavati, and Umbabat private nature reserves, each of which is composed of many private properties that have adopted the overall management plan of the APNR. Elephant numbers in the APNR have increased over a 10-year period. In 2002, the population was estimated at 952 individuals. In 2012, 1540 elephants were estimated, indicating an increase in density from 0.52 elephants per km² to 0.84 elephants per km² over 10 years (Peel 2014). A smaller and slower increase in elephant densities occurred in neighbouring KNP (0.40 elephants per km² to 0.70 elephants per km²) from 1904 to 2002 (Whyte, Van Aarde & Pimm 2003).

Overall, the APNR is characterised as a typical savanna ecosystem with a continuous grass understory and isolated trees (Scholes & Archer 1997). However, the vegetation within the APNR varies regionally. The eastern areas have dense *Colophospermum mopane* (mopane) woodland as well as isolated *A. nigrescens* and *S. birrea*. In other areas *Combretum apiculatum* (red bush willow), *L. schweinfurthii* and *Terminalia sericea* (silver cluster leaf) occur regularly (De Villiers 1994). Mean annual rainfall varies around 600 mm and temperatures average 22 °C throughout the year (Greyling 2004; Venter & Gertenbach 1986).



Source: Map by M. Henley

FIGURE 1: Map of South Africa showing the Associated Private Nature Reserves with the individual properties where surveys were conducted.

Tree selection and netting procedure

Properties in the APNR were selected based on the owner's interest in participating in the study. In 2004, at the onset of the study, 63 *Sclerocarya birrea* trees were tagged. By 2008, the study was expanded to include six properties, two more species, and 2915 tagged trees, of which 53% had been wrapped in wire netting (Figure 1). These trees were resurveyed in 2012 and data collected in that year were used for analysis. Trees were selected by species and size as determined by both the height and girdle width of the tree. *Sclerocarya birrea*, *A. nigrescens*, and *L. schweinfurthii* trees of greater than 5 m in height were tagged and approximately half were wrapped with wire netting. In addition, trees greater than 2 m in height with similar diameter at breast



Source: Photo by K. Derham

FIGURE 2: Mesh wire netting (13 mm) around a *Sclerocarya birrea* used to reduce elephant bark stripping.

height (DBH) were included if their height had been previously modified by elephant impact. *Sclerocarya birrea* and *A. nigrescens* were chosen because residents of the APNR expressed concern about these species in surveys conducted since 2003 in the APNR (Henley 2013). In addition, *L. schweinfurthii* trees are readily accepted as a food source in the dry months by elephants in the area (Greyling 2004).

Wire netting was wrapped around the trunk of the tree (Figure 2) about 50 cm off the ground to a height of about 230 cm and secured with fencing staples. On average 1.25 m of wire were used per tree. This amount of wire ensured that most of the area in which elephants primarily remove bark was covered (Stokke & Du Toit 2000). Average tusk entry height for trees in this study in 2004 was 120.4 cm \pm 35.6 cm ($n = 63$). Prior to using wire, the tree was inspected for any holes left by squirrels, nesting birds, or other animals, and if necessary holes were cut in the wire for these species. Wire netting was sometimes applied to trees that were already bark stripped by elephants and new impact was recorded based on the extent of wire-net penetration to access the bark beneath in comparison to previous survey data.

Assessment of elephant impact

A total of 95 of the trees surveyed in 2008 were located again in 2012. Of the 2772 relocated, 57 were dead with the cause of death not directly ascribed to elephants as only remains of the trees were found, and elephant impact from previous years of data collection was not severe enough to have caused death. Death in these cases was described as either because of fire where fire scarring was clearly visible or unknown causes. The recent mortality of some trees could be ascribed to wind toppling following storms with strong winds in the study area. Only those trees whose DBH could be recorded accurately (2668) were used for analysis (Table 1).

We used the following separate measures of elephant impact in the field: (1) bark stripping (BS), (2) branch breaking to access smaller plant parts (BBA), (3) main stem breaking (MS), and (4) uprooting (UR), as defined by Greyling (2004). During analysis, a fifth category, felling (Fell), was created by combining the categories MS and UR, which individually had small sample sizes. For each measure of elephant impact, a score between 1 and 10 was given based on its severity as adapted from Anderson and Walker (1974). In instances where multiple impact types occurred, each event was recorded separately. When two or more instances of the same

TABLE 1: The number of trees of each species with average diameter at breast height and cost of wire in the Associated Private Nature Reserves, South Africa.

Tree species	Number of trees		DBH (cm)		Cost R96.47 per tree: Wire
	No wire	Wire	No wire	Wire	
<i>Sclerocarya birrea</i>	563	789	31.2 \pm 12.1	42.5 \pm 13.3	R76114.83
<i>Acacia nigrescens</i>	309	548	42.2 \pm 12.9	46.4 \pm 13.4	R52856.56
<i>Lannea schweinfurthii</i>	409	50	31.2 \pm 15.1	41.4 \pm 12.8	R4823.50
Total	1281	1387	33.8 \pm 14.1	44.0 \pm 13.5	R133803.89

Note: DBH differed significantly between unprotected (33.8 cm \pm 14.1 cm) and protected trees (44.0 cm \pm 13.5 cm) (t -test, $t = -17.9$, $df = 2, 418$, $P < 0.001$) and was therefore used as a covariate in log linear analyses.

DBH, diameter at breast height.

type of impact were present, the most severe impact was recorded.

Impact from other animals such as black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), or Cape buffalo (*Syncerus caffer*) was differentiated based on the height and type of bark stripping or branch breaking and recorded separately from elephant impact. Such impact was rare (26 of the 1281 unprotected, tagged trees [2.0%] had been bark stripped by rhinoceros or Cape buffalo when sharpening their horns) and therefore damage from other animals was excluded from analysis. DBH was measured and recorded (in centimetres) for each tree. Tree height was also measured in the field but was highly correlated with DBH ($r = 0.64$, $P < 0.001$). Therefore, DBH was used as a proxy for overall tree size in analyses.

For bark stripping and branch breaking, impact scores included 1 (0%), 2 (< 1%), 3 (1% – 5%), 4 (6% – 10%), 5 (11% – 25%), 6 (26% – 50%), 7 (51% – 75%), 8 (76% – 90%), 9 (91% – 99%) and 10 (100%). Bark stripping percentage was determined by the proportion of the circumference of the tree that had been bark stripped, which is a method commonly used in other studies also considering this impact type (Anderson & Walker 1974; Helm *et al.* 2011). For branch breaking, the score was determined based on the percentage of all branches that had been broken by elephants. Scores were determined for MS and UR based on whether the tree survived the impact and if any new growth was present. A score of 1 was given to trees with no impact and a score of 10 given to trees with heavy elephant impact, resulting in the death of the tree (Henley 2013). Scores of 6, 7, 8, and 9 were given in situations where trees had their main stem snapped or had been uprooted to a varying degree by elephants but had not died. These scores were dependent on the amount of the upper stem still attached to the lower stem for main stem breakage and the angle of the uprooted tree for the uprooting category. The variable amounts of regrowth left after the impact incident also contributed to the overall assessment of the score. A further description of each score is provided in Greyling (2004) and Derham (2012).

Statistical analysis

To determine whether wrapping the tree in wire netting affected the likelihood that a tree would be bark stripped or incur any other type of impact by elephants, log linear analyses were performed. Because species are known to vary in their vulnerability to elephant impact, species was used as another factor in the log linear analysis. Since size (DBH) was significantly different between wire-net protected and unprotected trees (t -test, $t = -17.9$, $df = 2667$, $P < 0.001$) and among species (ANOVA, $F = 23.8$, $df = 2$, 2667 , $P < 0.01$), DBH was used as a covariate to account for the influence size might have on elephant impact. The mean DBH of wire-net-protected trees was $44.0 \text{ cm} \pm 13.5 \text{ cm}$, $n = 1387$ while the mean DBH of unprotected trees was $33.8 \text{ cm} \pm 14.1 \text{ cm}$, $n = 1281$. *Acacia nigrescens* were generally

the largest (mean DBH = $44.9 \text{ cm} \pm 15.2 \text{ cm}$, $n = 857$), compared with *Sclerocarya birrea* ($37.9 \text{ cm} \pm 13.4 \text{ cm}$, $n = 1352$) and *L. schweinfurthii* ($32.3 \text{ cm} \pm 14.0 \text{ cm}$, $n = 459$). Any significant results from the log linear analysis were investigated further. To assess differences in size between impacted and intact trees, Welch's t -tests to address unequal variance were performed. G-tests of independence were used to further investigate any differences by species (Sokal & Rohlf 2012).

To assess the effectiveness of wire netting in reducing the severity of elephant bark stripping, a G-test was performed with wire netting (2 levels) and score of bark stripping (10 levels). A G-test also was performed to analyse whether the distribution of overall elephant impact across classes differed between wire-net-protected and unprotected trees. For this analysis the highest impact score was recorded for each tree regardless of whether it came from bark stripping, branch breaking, or felling. For example, if a tree had bark stripping impact of class 3 and uprooting impact of class 8, the overall impact for the tree was recorded as class 8 for this analysis. All statistical tests were performed using R statistical software with a type I error rate of 0.05 (R Core Team 2014). All assumptions were addressed, and a Bonferroni's correction was used when necessary.

Results

Elephant impact was common in this study with 2381 out of 2668 (89%) trees being impacted by elephants in some way or the other (Table 2). A total of 74 unprotected trees (5.8%) and 213 protected trees (15%) did not have any elephant impact (Table 2). In total, 25% of unprotected trees were bark stripped by elephants, while only 1.7% of wire-net-protected trees were bark stripped by elephants (Table 2). DBH was not significant in determining the likelihood of bark stripping ($P = 0.08$); however, wire netting ($P < 0.001$) and species ($P = 0.03$) were significant (Table 3). *Acacia nigrescens* had significantly more bark stripping than *L. schweinfurthii* ($G = 36$, $df = 1$, $P < 0.001$), which had significantly more bark stripping than *S. birrea* ($G = 7.2$, $df = 1$, $P < 0.01$; Figure 3a). There was no significant interaction between species and whether a tree was protected by wire netting, meaning that regardless of species differences, wire netting was effective at reducing the number of trees that were bark stripped ($P = 0.75$; Table 3).

TABLE 2: The number and percentage of total trees in each category of elephant impact in the Associated Private Nature Reserves, South Africa.

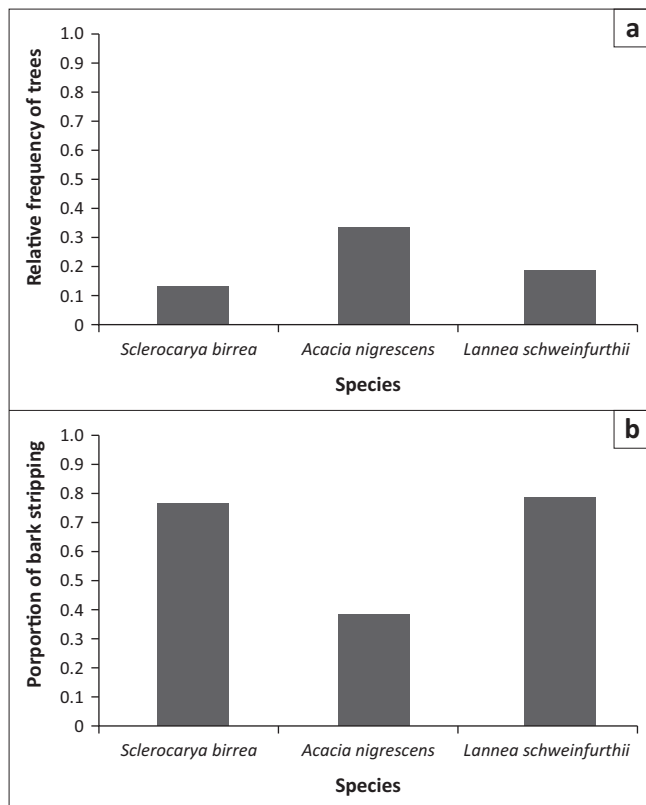
Impact	Number of trees: No wire	Percentage: No wire	Number of trees: Wire	Percentage: Wire
No impact	74	5.8	213	15
BS	321	25	24	1.7
BBA	878	69	894	64
MS	146	11	80	5.8
UR	253	20	119	8.6
Total number of trees	1281	-	1387	-

BS, bark stripping; BBA, branch breaking to access smaller plant parts; MS, main Stem breaking; UR, uprooting.

TABLE 3: Results of log linear analysis for the presence of bark stripping, branch breaking to access smaller plant parts, and felling (MS + UR) by elephants in the Associated Private Nature Reserves, South Africa.

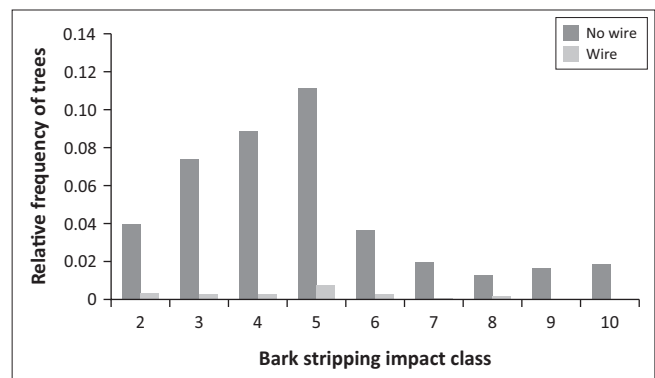
Model	df	BS residual deviance	BS <i>P</i>	BBA residual deviance	BBA <i>P</i>	Fell residual deviance	Fell <i>P</i>
Null	-	39.6	-	31.8	-	19.6	-
DBH	1	36.6	0.08	21.7	0.001	0.94	< 0.001
Species	2	4.88	< 0.001	1.39	< 0.001	0.54	0.82
Wire	1	0.10	0.03	0.92	0.49	0.11	0.51
Wire: Species	1	0.00	0.75	0.00	0.34	0.00	0.74

BS, bark stripping; BBA, branch breaking to access smaller plant parts; MS, main Stem breaking; UR, uprooting.

**FIGURE 3:** Relative frequency of bark stripping (a) and branch breaking (b) caused by elephant for *Sclerocarya birrea*, *Acacia nigrescens*, and *Lananea schweinfurthii* in the Associated Private Nature Reserves, South Africa.

In addition, the severity of bark stripping was reduced on trees protected by wire netting ($G = 55$, $df = 8$, $P < 0.001$) (Figure 4). The number of trees in all impact score categories was reduced with wire netting, and no tree wrapped with wire experienced impact in the highest two categories, 9 and 10 (Figure 4). Only three trees (0.2%) protected with wire netting were bark stripped more than 50% of the circumference of their trunk, compared with 85 (6.0%) without wire netting. In addition, no tree with wire netting was ring barked (i.e. class 10; 100% bark stripped), compared with 23 unprotected trees.

The presence or absence of wire netting was not a significant factor for explaining the occurrence of elephant impact other than bark stripping (branch breaking $P = 0.49$; felling $P = 0.51$; Table 3; Figure 3b). Branch breaking was recorded for 69% of unprotected trees and 64% of protected trees (Table 2). DBH had a significant effect on the occurrence of branch breaking ($P = 0.001$; Table 3), with smaller trees more likely to have their branches broken by elephants ($t = 3.80$, $df = 1788$, $P < 0.001$). In addition, species was an important factor



Note: Class 2 = < 1% of circumference of tree bark stripped; Class 3 = 1% – 5%; Class 4 = 6% – 10%; Class 5 = 11% – 25%; Class 6 = 26% – 50%; Class 7 = 51% – 75%; Class 8 = 76% – 90%; Class 9 = 91% – 99%; Class 10 = 100%.

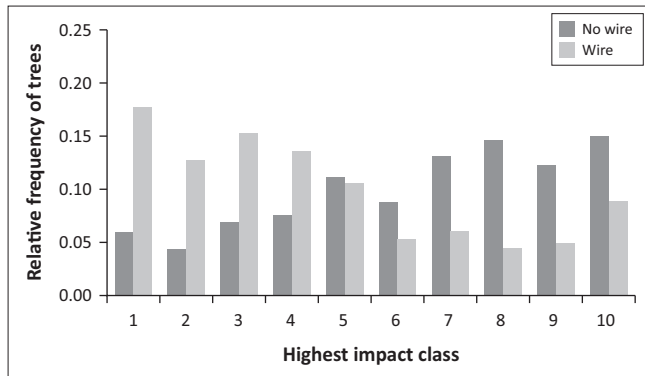
FIGURE 4: The relative frequency of trees in each bark stripping class for wire-net protected and unprotected trees in the Associated Private Nature Reserves, South Africa.

influencing branch breaking ($P < 0.001$; Table 3). *Acacia nigrescens* had significantly fewer branches broken compared with *S. birrea* ($G = 346$, $df = 1$, $P < 0.001$) and *L. schweinfurthii* ($G = 208$, $df = 1$, $P < 0.001$) (Figure 3b). There was no significant difference in branch breaking between *S. birrea* and *L. schweinfurthii*. DBH was a significant factor in influencing whether a tree had been felled ($P < 0.001$; Table 3). Felled trees were significantly smaller in DBH than trees that remained standing ($t = 11.3$, $df = 954$, $P < 0.01$). Although 15% of trees without wire netting were felled and only 7% with wire netting suffered from this impact, once DBH was accounted for, species and treatment were not significant factors (Table 3).

Although wire netting was not successful at significantly reducing the proportion of trees that had their branches broken or were felled by elephants, it did have a significant influence on the distribution of the level of impact ($G = 73.8$, $df = 9$, $P < 0.001$; Figure 5). Trees that were protected with wire netting were more likely to experience lower levels of elephant impact than unprotected trees. Sixty two per cent of the time the highest impact recorded was branch breaking. Therefore, it appears that wire netting reduced the degree of branch breaking in trees that were impacted in this way by elephants.

Discussion

Wire netting was effective at reducing the relative frequency and severity of bark stripping by elephants in this study. Since high levels of bark stripping are known to affect tree survival (Helm *et al.* 2011; Ihwagi *et al.* 2009), wire netting could prevent mortality by decreasing both the number of trees that are bark stripped by elephants and the occurrence



Note: Branch breaking was recorded for 1745 trees as their highest elephant impact, while 1270 trees had felling and 742 trees had bark stripping as their highest elephant impact. Some trees had more than one type of elephant impact in which case only the highest impact class was used in the analysis irrespective of the type.

FIGURE 5: The relative frequency of trees in each impact class where the highest level of impact by elephants was recorded within the Associated Private Nature Reserves, South Africa.

of severe impact. Although wire netting did not significantly decrease the frequency of branch breaking or felling, it did reduce the occurrence of high levels of all types of impact. Trees that are likely to experience severe elephant impact, specifically ringbarking, main stem breaking, or uprooting are susceptible to mortality (O'Connor *et al.* 2007) and therefore wire netting could help these trees survive in areas with high elephant densities.

Along with the absence or presence of wire netting, tree species and size were important factors in explaining damage for some measures of impact. DBH did not significantly affect the frequency of bark stripping; however, this could be because most of the tagged trees were of a similar size. If we included a wider range of tree sizes in the study, then it is possible that some sizes of trees would benefit more from wire netting. For example, Smallie and O'Connor (2000) found that trees taller than 4 m were selected by elephants for bark stripping. Further research would be needed to see if smaller trees would also benefit from wire netting and how the wire netting of such trees could accommodate girth expansion over time. *Acacia nigrescens* had high levels of bark stripping suggesting it might be preferred by elephants for this type of impact. Physical properties of the bark itself may account for the differences in frequencies of bark stripping between the species (O'Connor *et al.* 2007). In addition, elephants are known to bark strip larger trees and this result might also be because *A. nigrescens* were significantly larger than *S. birrea* and *L. schweinfurthii* in this study (Boundja & Midgley 2010; Smallie & O'Connor 2000). Since wire netting was effective regardless of species, it could benefit all three of the species assessed in this study. However, it might be particularly useful in reducing elephant bark stripping in preferred species such as *A. nigrescens*.

In contrast to other methods of reducing elephant impact such as culling and altering water-surface availability that focus on reducing elephant numbers or altering spatial distribution patterns, wire netting instead attempts to reduce impact by protecting the trees themselves. Some research has used elephant enclosures to study the relative impact of

elephants on trees (Western & Maitumo 2004). However, as a management tool these enclosures also exclude other large herbivores such as giraffe from accessing the trees (Goheen & Palmer 2010; Western & Maitumo 2004). In contrast, wire netting maintains the functionality of the trees for other organisms in the ecosystem by allowing them to access the trees for refuge, shade, food, and other activities. Wire netting is a relatively low maintenance strategy of reducing elephant impact. In the current system, the wire netting did not need to be replaced from the time it was applied in 2004 until the last survey in 2012 and very little maintenance was required. Depending on the scale at which trees are wire-net protected, it could be cost-effective. Electric fencing has been used to keep elephants out of specific areas but it is more expensive and can be problematic to maintain (Kiokoe *et al.* 2008). In addition, wire netting wrapped around the trunk of a tree is certainly less visible to tourists than electric fencing.

Conclusion

This study aimed to assess the effectiveness of wire netting in reducing elephant impact on trees in the APNR. We found that wire netting reduced the proportion and severity of elephant impact and contributed to the survival of trees. As elephant densities in the APNR and other areas continue to increase, there will need to be strategies to maintain these iconic and valuable large tree species. In such areas, the use of wire netting could serve to alleviate elephant impact.

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Competing interests

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

K.D. performed most of the fieldwork and was responsible for data analysis and write up. M.D.H. was responsible for experimental and project design and all field surveys prior to 2012. M.D.H. and B.A.S. made conceptual and editorial contributions.

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