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African honeybees as a mitigation method for elephant impact on trees

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ABSTRACT

Conservation managers are concerned about the impact that African elephants (Loxodonta africana) have on large tree species, necessitating the need for mitigation methods. Elephants actively avoid contact with African honeybees (Apis mellifera subsp. scutellata), staying clear of crop fields surrounded by beehive fence-lines and moving away from the sounds of swarming honeybees. Therefore, our objectives were to test whether the presence of beehives in trees influenced the likelihood of the tree receiving elephant impact, and compare these results to wire-netted (method used to prevent bark-stripping) and control (no treatment) trees. We selected a tree highly sought after by elephant, the marula tree (Sclerocarya birrea subsp. caffra), as our study species. We also assessed whether elephants avoided areas with marula trees containing beehives. Finally we provide a comparison of the financial costs of the beehive and wire-netting mitigation methods. We hung 50 active beehives in 50 trees, with 50 dummy beehives hung from branches on the opposite ends of each tree's main stem. We wire-netted another 50 trees and then assigned 50 trees as a control. Elephant impact on all 150 trees was measured prior to the addition of treatments and then post-treatment addition for 9 months. 54% of the control trees received some form of elephant impact, in comparison to 28% of the wire-netted trees and only 2% of the beehive trees. Wire-netting protected trees against bark-stripping but did not prevent elephants from breaking branches. Beehives proved to be the more effective mitigation method for elephant impact on large trees, although the presence of beehives did not prevent elephants from moving through the study site. The financial cost and maintenance required for the beehive mitigation method are greater than that of wire-netting, but the beehives can provide honey as an additive benefit on a small-scale usage level.

1. Introduction

Conservation strategies of enclosing African elephant (*Loxodonta africana*) populations into protected areas have raised concerns over the impact that increasing elephant densities may have on large trees (Shannon et al., 2008; Asner et al., 2015; Cook et al., 2017). These concerns include the potential ecological (Vogel et al., 2014; Asner et al., 2015) and aesthetical (Edge et al., 2017) effects of such impact. Current management strategies apply mitigation methods to alter elephants' spatial and temporal access to resources (e.g., SANParks, 2012). One such method that has been used to mitigate elephant impact on large trees is wire-netting (Derham et al., 2016). Wire-netting involves wrapping chicken-mesh around the main stem of a tree in an attempt to prevent severe bark-stripping. Wire-netting is cost-effective, applicable at large spatial scales, and has prolonged the survival rate of large trees in the Klaserie, Timbavati, and Umbabat Private Nature Reserves

(Derham et al., 2016). However, wire-netted trees are still vulnerable to branch breakage, main stem snapping and uprooting by elephants (Derham et al., 2016) leaving the tree vulnerable to invasion by woodborers (Coetzee et al., 1979). Therefore, for individually selected trees in need of protection, the proposed use of African honeybees (*Apis mellifera* subsp. *scutellata*) may prove more effective.

Previous research has provided evidence that African honeybees can be used as a mitigation method for elephant impact on vegetation (Vollrath and Douglas-Hamilton, 2002). The African honeybee is a particularly aggressive honeybee species (Alaux et al., 2009). The stings of a swarming colony pose a threat to sensitive areas of an elephant, including behind the ears, around the eyes, and within and under the trunk (Buss and Estes, 1971; Jacobson et al., 1986). Elephants display a variety of distressed behaviours to the pre-recorded sounds of "buzzing" honeybees (King et al., 2007), and have been successfully deterred from crop raiding through the design of beehive fence-lines consisting of

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Received 13 July 2017; Received in revised form 21 October 2017; Accepted 21 November 2017 Available online 23 November 2017 0006-3207/ © 2017 Elsevier Ltd. All rights reserved. connected active and dummy beehives surrounding crop fields (King et al., 2011, 2017). The use of only dummy (unoccupied) beehives to protect trees from elephant impact has had limited success (Vollrath and Douglas-Hamilton, 2002; Karidozo and Osborn, 2005), whilst elephants may still impact large trees with only a single active (occupied) beehive hanging from one branch (LE. King, personal communication, March 12, 2015). However, it has yet to be investigated whether the presence of both an active and a dummy beehive in a single tree can provide protection against elephant impact. Furthermore, given the costs associated with active beehives, our design aimed to test whether elephants would still impact a tree if one beehive was active and the other beehive was a dummy. Elephants display selective preferences for some large tree species, with marula trees (Sclerocarva birrea subsp. caffra; Anacardiaceae) in particular, being one of the preferred forage choices (Greyling, 2004; Shannon et al., 2008). Elephant impact on marula trees has been researched in South Africa because of the tree's cultural, economic, and ecological importance (Shackleton et al., 2002; Helm and Witkowski, 2013). In protected areas, the leaves of marula trees provide a food source for browsers and insects, whilst the fruit on the female trees are eaten by species such as elephants, warthog (Phacochoerus africanus), chacma baboon (Papio ursinus) and vervet monkeys (Cercopithecus aerhiops) (Shackleton et al., 2002). Marula trees also provide shade and habitat for various mammals, birds, insects and plants (Hall et al., 2002; Vogel et al., 2014). In South Africa's Greater Kruger National Park (Greater KNP), where elephant densities are continuously increasing (Chase et al., 2016), marula trees have been severely bark-stripped, toppled, or had their main stems snapped by elephants (Coetzee et al., 1979; Helm and Witkowski, 2013; Cook et al., 2017). Furthermore, recent studies have reported declines in marula tree numbers by around 25% in some areas of the Greater KNP, as a result of elephant impact (Helm and Witkowski, 2013; Cook et al., 2017). Therefore, our objectives are to test whether the presence of beehives in trees influences the likelihood of the tree receiving elephant impact, and compare these results to wire-netted and control (no treatment) trees. We also assess whether elephants avoid areas with trees containing beehives. Finally we provide a comparison of the financial costs associated with the beehive and wire-netting mitigation methods. We predict that the beehive mitigation method will provide trees with greater protection against elephant impact in comparison to wire-netting. However, the high costs and maintenance involved with the beehive mitigation method may restrict the method's usage, making it more applicable for selective tree individuals, depending on the resources that the protected area's management is willing to mobilise towards the mitigation method.

2. Material and methods

2.1. Study area

We conducted our study in a 30 ha experimental site within Jejane Private Nature Reserve (JPNR), a protected area that opened up to the Greater KNP in 2013 (S24.29045; E30.97664, Fig. 1). The 30 ha experimental site was used to minimise external factors which could influence a tree's susceptibility to elephant impact, such as distance to water (Chamaillé-Jammes et al., 2009). JPNR was an ideal study site because of the high density of adult marula trees (Helm and Witkowski, 2012), and the high mortality rates of marula trees as a result of elephant impact (Cook et al., 2017). Furthermore, JPNR has abundant artificial waterholes (1 waterhole per 1.78 km² in the wet season and 1 per 3.35 km² in the dry season; Cook et al., 2017), an important attractant for elephants (Smit et al., 2007). JPNR receives a mean annual rainfall of 400–600 mm and is located in the Granite Lowveld vegetation unit (SVI 3) in the Savanna biome (Mucina and Rutherford, 2006).

2.2. Baseline elephant impact assessments

We conducted baseline assessments on 150 standing adult marula trees (> 5 m in height) prior to the adoption of mitigation methods. We selected trees further than 15 m from a roadside to avoid the effect that roads can have on a tree's susceptibility to elephant impact (Coetzee et al., 1979). We selected trees > 7 m apart (main stem to main stem) to avoid, once treatments were added, the presence of beehives in one tree preventing elephant impact on other trees (elephants have been recorded approaching beehive fence-lines within 2 m; King et al., 2011).

The trees assessment followed methodology adapted from Henley (2013). In particular we georeferenced each tree's location with a Global Positioning System (GPS; model GPSmap 62st) and recorded stem diameter at breast height (DBH) into the following size classes: Class 1 (20-29 cm), Class 2 (30-39 cm), Class 3 (40-49 cm), Class 4 (50-59 cm), and Class 5 (60-69 cm). Tree height was measured with the VolCalc digital photography method (Barrett and Brown, 2012) and grouped into two size classes: Class 1 (5-8 m), and Class 2 (8-11 m). Because marula trees are dioecious, we identified the sex of each tree by searching for fruit endocarps below the tree's canopy, classifying trees with endocarps present as female trees (Helm et al., 2011). We assessed impact-types on each tree, as defined by Walker et al. (1986) and modified by Greyling (2004), into tree-fate classes (Table 1). Barkstripping was measured as the percentage of bark stripped around the tree's main stem circumference; and primary branch breakage was calculated as the proportion of primary branches broken off the tree. We assessed uprooting, main stem snapping, and secondary branch breakage during post-baseline assessments after the addition of mitigation methods to the trees.

2.3. Mitigation methods

We divided the 150 trees into three groups: 50 beehive trees, 50 wire-netted trees, and 50 control trees. Trees were distributed proportionately across the 3 mitigation methods according to their DBH to avoid bias in the probability of a DBH class being preferred by elephants ($\chi_2^2 = 7.42$; p = 0.49; n = 150).

2.3.1. Beehives

We built 100 beehives (50 active and 50 dummy) in the form of modified bait hives from 20 mm laminated pine shelving wood and coated twice with Waksol, a solvent-based wax preservative for wood (Fig. 2a). We hung nylon ropes from the 50 beehive trees and connected the 50 dummy beehives to the ropes. We then transported 50 honeybee colonies into JPNR and transferred their frames into the 50 active beehives. The 50 active beehives were hung overnight (10 pm–5 am) from 13 to 14 December 2015, so that each beehive tree had one active and one dummy beehive (Fig. 2a). Beehives were hung 2 m above the ground (adult elephant eyelevel). Engine grease was smeared along the nylon ropes to prevent ant invasion, however, the grease was replaced by Plantex glue which proved to be more effective at protecting beehives from ants.

We assessed the presence or absence of honeybee colonies on a weekly basis (15 December 2015–28 September 2016). Because of the prevalent drought conditions of 2015–2016 in South Africa, we implemented a feeding regime for the honeybee colonies. We placed 16 feeder stations within the study site in January 2016, providing the honeybees with sugar water (ratio 1:3), which was refilled every 3 days. As of 30 May 2016, we added a specialised nectar feed solution (*Booster Bee*, Johannesburg, South Africa) into the sugar water to provide a nectar supplement during the winter months. A pollen substitute (*Booster Bee*, Johannesburg, South Africa) was simultaneously given to each active colony once a week. We changed the feeder station locations in accordance to which beehives were active. The artificial feeding of honeybees is carried out in elephant-honeybee research projects in



Fig. 1. Location of Jejane Private Nature Reserve (JPNR) within the Greater Kruger National Park (KNP), South Africa. The beehive and control sites were situated in the western section of JPNR, > 500 m from any human settlements. The lines within the beehive and control sites represent elephant dung transects.

Kenya (LE. King, personal communication, August 11, 2017) and Sri Lanka (personal observation).

2.3.2. Wire-netting

We wrapped chicken-mesh (13 mm diameter, 1.8 m tall) twice around the main stems of 50 trees to form a rigid cage-like structure, starting 50 cm above the ground (Fig. 2b). The ends of the chickenmesh were stapled to the tree trunk with 25 mm wire-fencing staples. All 50 trees were wire-netted over the period of a week (31 October 2015–07 November 2015).

2.4. Elephant impact and mitigation method efficiency

We monitored elephant impact on the 150 trees once a month (January 2016–December 2016) to record changes to the scores from the baseline tree-fate class assessments for bark-stripping and primary branch breakage. We used the same assessment guidelines as described above (Table 1). We also recorded uprooting, main stem snapping, and secondary branch breakage (Table 1).

To investigate whether the mitigation method affected the likelihood (presence/absence) of a tree receiving any form of elephant impact; or bark-stripping only; or branch breakage only (primary and secondary branch breakage), we performed log linear analyses through a generalised linear model with a binomial distribution and a logit-link function from the 'rcompanion' package (Mangiafico, 2015). Tree height, which can affect a tree's susceptibility to elephant impact, was used as a second explanatory variable. We used Pearson's chi-squared tests of independence and post-hoc pair-wise chi-square tests of independence to further investigate differences between mitigation methods and height categories. As DBH can influence a tree's susceptibility to being bark-stripped (Vogel et al., 2014), we included DBH as an explanatory variable for the likelihood of bark-stripping. Additionally, as female marula trees may be more susceptible to elephant impact in comparison to males (Hemborg and Bond, 2007), we used a Pearson's chi-square test of independence to investigate whether there was a significant difference between the number of female and male trees receiving impact. We calculated the weighted average impact scores of each tree for bark-stripping, primary branch breakage, and secondary branch breakage from the mean number of trees per tree-fate class for each mitigation method (Table 1). Weighted average impact scores were calculated for both the baseline and the final (September 2016) assessments. We then used Wilcoxon signed-rank tests to assess changes in weighted average impact scores between the baseline and final assessments for the three impact-types within each mitigation method. All statistical analyses were performed with R statistical software (R v. 3.2.2, R Development Core Team, 2016).

2.5. Elephant dung transects

We performed weekly dung transects (January 2016–September 2016) to compare elephant presence in the beehive site versus a control site directly north in the same road loop within JPNR (Fig. 1). Elephant dung was used as a proxy for elephant presence. We set six transects (300 m × 40 m) within the beehive site, each separated by 150 m, whilst 6 replica transects were set in the control site. Each transect had a searching effort of 15 min, where we recorded the GPS co-ordinates of any new elephant dung piles which had not been recorded in the previous survey. Collective dung piles by breeding herds or coalitions of bulls were not separated in the analysis, as only one breeding herd moved through the study site. We used a 2-sample *t*-test to assess differences between the mean number of monthly dung sample sightings within the beehive and control sites' transects.

2.6. Financial costs comparisons

We calculated the financial costs on an individual tree basis. We divided costs into "Setup costs" and "Additional running costs". Setup costs included all construction expenses associated with the mitigation method (materials, labour), whilst Additional running costs included

Impact-type	Tree-fate classes									
	1	2	3	4	5	9	7	8	6	10
Bark-stripping Primary branch breakage	No damage No damage	< 1% > 0-25%	1–4% 26–50%	5-10% 51–99%	11–25% 100%	26-50%	51-75%	%06-90	91–99%	100%
Uprooting	No damage	Tree alive, roots in ground, just leaning over (> 0–25%)	Tree pushed onto ground but is alive and has all roots in ground (26–50%)	Tree alive but has half of the roots in the ground and half of the roots exnosed in the air (50–99%)	Tree has been uprooted (all of the tree's roots are in the air) (100%)					
Main stem snapping	No damage	Main stem has been snapped but is in a re-coppicing state (>0-25%)	Crown of tree is still attached to the main stem and the tree is still aive (76–00%)	Tree is still alive but not in a re- coppicing state (50–99%)	Tree has subsequently died from main stem breakage (100%)					
Secondary branch breakage	No damage since baseline assessment	New damage since baseline assessment								

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scoring system for elephant impact-types and tree-fate classes on large trees, as defined by Walker et al. (1986) and modified by Greyling (2004).

Table 1

further expenses post-mitigation method setup. Setup costs for the wirenetting included the chicken-mesh, staples and labour. Setup costs for the beehives included the beehive materials and manufacturing labour, as well as the purchasing of one live honeybee colony per tree. There were no Additional running costs for wire-netting. The costs of supplementary food for the honeybees were calculated on a monthly basis as Additional running costs and were divided by the number of beehive trees. We then estimated the financial costs for a 10-year period to investigate the longevity-financial relationship of the mitigation methods. Financial costs excluded interest rate increases. For beehive Setup costs, we estimated that the wooden beehives would need replacing every 3 years, and so construction costs were multiplied by three over a 10-year period. For wire-netting, we estimated that the chicken-mesh would need replacing once every 10 years (Derham et al., 2016).

3. Results

3.1. Beehive occupancy

Of the 50 active beehives, 26 were abandoned within the first 4 months as a result of ant invasions or factors related to the drought. Active beehive numbers slowly stabilised during the second half of the study period, coinciding with the addition of nectar and pollen substitute into the feeding regime. 22 beehives were still active after 9 months.

3.2. Elephant impact and mitigation method efficiency

3.2.1. Impact (all impact-types)

The number of trees receiving new impact differed significantly between the mitigation methods ($\chi_2^2 = 33.53$; p < 0.0001; n = 150). Only one beehive tree received new impact (secondary branch breakage, Table 2), significantly less than control (n = 27) $(\chi_1^2 = 31.01; p < 0.0001; n = 100)$ and wire-netted (n = 14) $(\gamma_1^2 = 11.29; p < 0.05; n = 100)$ trees. One control tree was killed as a result of main stem snapping (class 3 for main stem snapping) and three control trees had all of their primary branches removed (class five for primary branch breakage). No heavy impact (> 50% for bark-stripping and primary branch breakage) was recorded on beehive and wirenetted trees. Tree height was a significant determinant of a tree receiving elephant impact, with elephants showing a greater preference for trees in height class 1 (5-8 m) in comparison to height class 2 (8–11 m) (χ_1^2 = 6.05; p < 0.05; n = 150). Height class preference however, did not differ across mitigation methods ($\chi_2^2 = 4.19$; p = 0. 12; n = 150). The proportion of female trees receiving impact (25 of 123) was significantly less than that of male trees (17 of 27) $(\chi_1^2 = 19.97; p < 0.00001; n = 150)$. However, as no fruit was recorded on the trees during the study period, and due to the low number of sampled male trees, the effect of sex on elephant impact was not investigated further.

3.2.2. Bark-stripping

The number of trees receiving bark-stripping differed significantly between mitigation methods ($\chi_2^2 = 30.88$; p < 0.0001; n = 150). There was new bark-stripping on 13 control trees, whilst no new bark stripping was recorded on behive and wire-netted trees (Table 2). The weighted average impact score for bark-stripping on the control trees increased significantly over the study period (Table 2). DBH size class significantly influenced the likelihood of a control tree being bark-stripping occurring on trees in DBH size class 2 (30–39 cm; n = 8). However, the effect of DBH across treatments could not be tested as no bark-stripping occurred on behive and wire-netted trees.



Fig. 2. (a) Beehive mitigation method: two nylon ropes with looped-ends were hung and stapled from each branch so that the looped-ends were 2 m above the ground (adult elephant eyelevel). One insulation lambdaboard was placed on the roof of each active beehive for insulation. (b) Wirenetting mitigation method: chicken-mesh (13 mm diameter, 1.8 m height) was wrapped around the main stem twice and stapled at the ends, creating a rigid cage-like structure.

3.2.3. Branch breakage

The number of trees with new broken branches differed significantly between mitigation methods ($\chi_2^2 = 16.92$; p < 0.001; n = 150), with new broken branches on 19 control trees, significantly more than beehive trees (n = 1) ($\chi_1^2 = 18.06$; p < 0.01; n = 100). The number of wire-netted (n = 14) and control trees with new broken branches did not differ significantly ($\chi_1^2 = 0.41$; p = 0.51; n = 100). For control trees, there were significant increases in the weighted average tree-fate classes for both primary and secondary branch breakage (Table 2). Only secondary branch breakage increased significantly for wire-netted trees (Table 2). Tree height was a significant determinant for a tree having its branches broken off, with a greater proportion of new broken branches on trees in size class 1 (5–8 m) compared to size class 2 (8–11 m) ($\chi_1^2 = 4.03$; p < 0.05; n = 150). Height class preference however, did not differ across mitigation methods ($\chi_2^2 = 4.68$; p = 0.42; n = 150).

3.3. Elephant dung transects

There was no significant difference between the mean number of monthly dung sample sightings between the beehive and control sites (2-sample *t*-test: $t_{(16)} = -0.28$; p = 0.79; n = 9), with 43 dung sample sightings within the beehive site (mean \pm SE = 4.78 \pm 1.30) and 47 in the control (mean \pm SE = 5.22 \pm 0.96).

3.4. Financial costs comparisons

The beehive mitigation method was more expensive than wirenetting, with higher costs required for the Setup process, as well as the Additional running costs (Table 3). The differences in costs between the mitigation methods is further amplified in the 10-year estimate because of the continual need to replace beehives (Table 3).

Table 2

Weighted average impact scores (\pm SD) for marula trees during the baseline and final assessments across the impact-types for the three mitigation methods in Jejane Private Nature Reserve.

Impact-type	Control $(n = 50)$		р	Wire-netting $(n = 50)$			р	Beehive $(n = 50)$			р	
	Number of trees impacted	Baseline	Final assessment		Number of trees impacted	Baseline	Final assessment		Number of trees impacted	Baseline	Final assessment	-
Bark-stripping	13	1.50 (0.16)	1.80 (0.18)	**	0	1.72 (0.19)	1.72 (0.19)	NS	0	2.08 (0.26)	2.08 (0.26)	NS
Primary branch breakage	8	1.16 (0.07)	1.60 (0.18)	*	1	1.58 (0.14)	1.62 (0.14)	NS	0	1.38 (0.11)	1.38 (0.11)	NS
Secondary branch breakage	11	1.00	1.22 (0.06)	**	13	1.00	1.26 (0.06)	**	1	1.00	1.02 (0.02)	NS

NS - Non significant.

* p < 0.05.

** p < 0.01.

Table 3

Financial costs (US Dollars) per marula tree for the beehive and wire-netting mitigation methods over 1-year and 10-year periods.

Mitigation method	gation method Time scale			Set up cost per	Additional runnin	Total overall cost per		
		Construction	Honeybee colony	liee	Sugar water per tree	Nectar and pollen substitute per tree		
Beehive tree	1 year estimate per tree	\$62.50	\$27.75	\$90.25	\$18	\$31	\$139.25	
	10 year estimate per tree	\$187.50	\$27.75	\$215.25	\$180	\$310	\$705.25	
Wire-netted tree	1 year estimate per tree	\$10.50	/	\$10.50	/	/	\$10.50	
	10 year estimate per tree	\$21	/	\$21	/	/	\$21	

4. Discussion

New elephant impact was recorded on 27 control trees, 14 wirenetted trees and one beehive tree. The only beehive tree to receive elephant impact had secondary branches broken. Wire-netting prevented bark-stripping but was still susceptible to branch breakage.

This is the first known study to make use of a combination of both active and dummy beehives as a mitigation method for elephant impact on large trees. In the original elephant-honeybee experiment by Vollrath and Douglas-Hamilton (2002), 24 of the 30 Vachellia xanthophloea with inactive beehives were impacted, whilst none of the 6 trees with active beehives received impact. Our study provides evidence that the combination of active and dummy beehives on a single large tree can be highly effective at mitigating elephant impact, particularly as our design was tested on marula trees which are highly sought after by elephants (Greyling, 2004; Shannon et al., 2008). Furthermore, these results have been recorded in an area of the Greater KNP that has lost a quarter of its adult marula tree population in three years as a result of elephant impact (Cook et al., 2017). The high mortality rate of marula trees is likely due to an initial influx of bull elephants into JPNR in 2013 when JPNR was incorporated into the Greater KNP (Peel, 2015; Cook et al., 2017). Bull elephants tend to have a greater impact on trees in comparison to cows and calves, breaking branches and pushing over stems to access browsing material, or for 'confidence building' and muscular training (Barnes et al., 1994; Midgley et al., 2005). The lack of impact on trees with both dummy and inactive beehives (active beehive which had been abandoned), suggests that a potential combination of the smell from the inactive beehives, as well as the beehives' swinging motion was still effective at mitigating elephant impact. Elephants have a well-developed sense of smell (Laws, 1970) and may have been deterred from approaching and disturbing trees containing beehives, regardless of the presence of honevbees. African honevbee alarm pheromones have also recently been analysed (Nouvian et al., 2016), and so the possibility exists that elephants can detect these pheromones because of their acute olfactory senses, and may respond to the artificial release of the synthesised pheromones to the same extent as to the honeybees themselves. Whilst the attractant of fruits on female trees could not be tested in this study as a result of the prevailing drought conditions (see Hemborg and Bond, 2007), the opportunity exists to evaluate the success of the beehive mitigation method during a wetter period. However, previous research in JPNR has found no significant difference in elephant impact on male and female marula trees (Cook et al., 2017), with similar results recorded in the Greater KNP by Gadd (2002).

The only impacted beehive tree had secondary branches broken off and the dummy beehive ripped out of the tree, with tracks of an adult elephant bull found 3 m from the tree's main stem. This impact took place on a tree with an active beehive. A musth elephant bull was observed in the beehive section of the experimental site 3 days after the incident (personal observation), and as musth bulls are aggressive in nature (Poole and Moss, 1981), their reaction to a beehive may change when in this intensified reproductive state. However, the success of beehives against elephant impact, in terms of preventing the removal of bark and primary branches, is important for the long-term survival of trees. The removal of bark and branches render trees vulnerable to invasions by wood-borers and fungi, which lead to the gradual deterioration of trees from the inside (Cowie et al., 1989). These trees are eventually hollowed-out and become more vulnerable to further elephant impact or strong winds (Jacobs and Biggs, 2002).

As this was the first year that our experiment was carried out, it still remains to be seen whether elephants will learn for example, that the side of a tree with a dummy beehive is a safe foraging locality, provided that the active beehive is not disturbed, or that a tree with two inactive beehives is safe from which to forage (Vollrath and Douglas-Hamilton, 2002). In Kenya, farms with low occupancy levels of active beehives have experienced more breakthrough events in comparison to farms with high occupancy levels (King et al., 2017). Long-term monitoring will be required to test these hypotheses. Furthermore, whilst the combination of one active and one dummy beehive was successful at mitigating elephant impact on marula trees, further studies are required on this method's efficiency against impact on other sought-after or protected tree species. For example, there are conservation concerns surrounding the impact that elephants have on baobab trees (Adansonia digitata) in protected areas (Edkins et al., 2008). The hanging of a single active and dummy beehive on either side of a tree with as large a main stem diameter as a baobab tree (up to 9 m, Coates Palgrave, 2002) may not be effective at mitigating elephant impact. New designs consisting of various combinations of active and dummy beehives will need to be tested for trees of various sizes if managers wish to implement the beehive mitigation method for elephants. Our initial findings also suggest that the presence of beehives in trees only results in the elephants avoiding those particular trees, rather than entire area containing beehives. However, elephant spatial distances to beehives may vary in accordance to beehives activity levels, with Ngama et al. (2016) finding that elephants are more likely to avoid beehives with high activity and defensive levels.

Wire-netting was effective at preventing bark-stripping, but these trees were still susceptible to branch breakage which increases a tree's vulnerability to woodborer invasions (Coetzee et al., 1979). Elephants may also be able to challenge wire-netting by ripping off the chicken-mesh (Henley, 2013), however, this is less likely to occur when the chicken-mesh diameters are small (13 mm) and more difficult for an elephant's tusks to penetrate. One wire-netted tree was also used as a rubbing post by an elephant during this study, evident by mud smeared along the chicken-mesh. It has not yet been tested whether the uneven surface of the chicken-mesh makes for an attractive rubbing surface, thereby increasing the probability of heavier elephant impact if the chicken-mesh were to be removed over time.

The setup cost of placing an active and dummy beehive in a tree was far greater than that of wire-netting. Beehives also had additional feeding costs. Furthermore, we calculated the mean costs of 50 trees per mitigation method, and so individual tree prices may still be slightly higher. The differences in the financial costs of the beehive and wirenetting mitigation methods, as well as how successful each method is against elephant impact, necessitates a management trade-off. Beehives are highly effective against elephant impact, and active beehives can also produce honey that can be sold to offset part of the costs (King et al., 2011, 2017). In Kenya for example, farmers have recorded financial profits of \$5 per 1 kg of honey (King et al., 2017). However, the beehive mitigation method is labour intensive with maintenance required for the wooden beehives and for potentially feeding the honeybees. These costs were specific for the use of beehives made from laminated pine shelving wood, as well as for feeding honeybees in a study site receiving a mean annual rainfall of 400-600 mm. Modern wood-free beehives, although initially more expensive to install, would help reduce replacement costs and promote honey production, whilst sites with a higher mean annual rainfall may require less manual feeding for the honeybees.

Beehives in trees may also be aesthetically unpleasing to tourists and dangerous if disturbed. As the use of beehives for deterring elephants is included in the elephant management plan of the Greater KNP (SANParks, 2012), careful planning is therefore required when deciding on beehive locations. Furthermore, trees that are designated for beehives should not be in areas of regular fire burn practices, or in the vicinity of electric fences and pylons, as this could result in the honeybees absconding from the beehives (Hepburn, 2006). Wire-netting has no additional benefits and is not effective against all forms of elephant impact. However, wire-netting is relatively cheaper, requires little maintenance post-installation, and is less visible to tourists. Wirenetting also has greater longevity, provided that the chicken-mess is not weakened by elephants, or chacma baboons do not climb and pull the chicken-mesh out of the tree, or the chicken-mesh is correctly placed and stapled to the tree (Derham et al., 2016).

5. Conclusion

We therefore suggest that the low costs and relative lack of maintenance associated with wire-netting renders it highly applicable for large-scale usage. The greater financial costs and maintenance required for the beehives may limit this mitigation method to selectively important trees in need of protection (provided that financial and logistical support is available), and would be more successful if associated with a financial revenue scheme from the harvested honey.

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References

Alaux, C., Le Conte, Y., Adams, H.A., Rodriguez-Zas, S., Grozinger, C.M., Sinha, S., Robinson, G.E., 2009. Regulation of brain gene expression in honey bees by brood

pheromone. Genes Brain Behav. 8 (3), 309–319. http://dx.doi.org/10.1111/j.1601-183X.2009.00480.x.

- Asner, G.P., Vaughn, N., Smit, I.P., Levick, S., 2015. Ecosystem-scale effects of megafauna in African savannas. Ecography 39 (2), 240–252. http://dx.doi.org/10.1111/ecog. 01640.
- Barnes, R.F.W., Barnes, K.L., Kapela, E.B., 1994. The long-term impact of elephant browsing on baobab trees at Msembe, Ruaha National park, Tanzania. Afr. J. Ecol. 32 (3), 177–184. http://dx.doi.org/10.1111/j.1365-2028.1994.tb00569.x.
- Barrett, A.S., Brown, L.R., 2012. A novel method for estimating tree dimensions and calculating canopy volume using digital photography. Afr. J. Range Forage Sci. 29

(3), 153-156. http://dx.doi.org/10.2989/10220119.2012.727471.

- Buss, I.O., Estes, J.A., 1971. The functional significance of movements and positions of the pinnae of the African elephant, *Loxodonta africana*. J. Mammal. 52 (1), 21–27. http:// dx.doi.org/10.2307/1378428.
- Chamaillé-Jammes, S., Fritz, H., Madzikanda, H., 2009. Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape. Ecography 32 (5), 871–880. http://dx.doi.org/10.1111/j.1600-0587.2009.05785.x.
- Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J.C., Djene, S.W., Elkan, P.W., Ferreira, S., Grossman, F., Kohi, E.M., Landen, K., Omondi, P., Peltier, A., Selier, J., Sutcliffe, R., 2016. Continent wide survey reveals massive decline in African savannah elephants. PeerJ 4, e2354. http://dx.doi.org/10.7717/peerj.2354.
- Coates Palgrave, K., 2002. Trees of Southern Africa. Struik Publishers, Cape Town, South Africa.
- Coetzee, B.J., Engelbrecht, A.H., Joubert, S.C.J., Retief, P.F., 1979. Elephant impact on Sclerocarya caffra trees in Acacia nigrescens tropical plains thornveld of the Kruger National Park. Koedoe 22 (1), 39–60. http://dx.doi.org/10.4102/koedoe.v22i1.650.
- Cook, R.M., Witkowski, E.T.F., Helm, C.V., Henley, M.D., Parrini, F., 2017. Recent exposure to African elephants after a century of exclusion: rapid accumulation of marula tree impact and mortality, and poor regeneration. For. Ecol. Manag. 401, 107–116. http://dx.doi.org/10.1016/j.foreco.2017.07.006.
- Cowie, R.H., Logan, J.W., Wood, T.G., 1989. Termite (Isoptera) damage and control in tropical forestry with special reference to Africa and Indo-Malaysia: a review. Bull. Entomol. Res. 79 (2), 173–184. http://dx.doi.org/10.1017/S0007485300018150.
- Derham, K., Henley, M.D., Schulte, B.A., 2016. Wire netting reduces African elephant (Loxodonta africana) impact to selected trees in South Africa. Koedoe 58 (1) (7pp.). https://doi.org/10.4102/koedoe.v58i1.1351.
- Edge, A., Henley, M.D., Daday, J., Schulte, B.A., 2017. Examining human perception of elephants and large trees for insights into conservation of an African savanna ecosystem. Hum. Dimens. Wildl. 22 (3), 231–245. http://dx.doi.org/10.1080/10871209. 2017.1298168.
- Edkins, M.T., Kruger, L.M., Harris, K., Midgley, J.J., 2008. Baobabs and elephants in Kruger National Park: nowhere to hide. Afr. J. Ecol. 46 (2), 119–125. http://dx.doi. org/10.1111/j.1365-2028.2007.00798.x.
- Gadd, M.E., 2002. The impact of elephants on the marula tree *Sclerocarya birrea*. Afr. J. Ecol. 40 (4), 328–336. http://dx.doi.org/10.1046/j.1365-2028.2002.00385.x.
- Greyling, M.D., 2004. Sex and Age Related Distinctions in the Feeding Ecology of the African Elephant, *Loxodonta africana* (PhD Thesis). University of the Witwatersrand, Johannesburg, South Africa.
- Hall, J.B., O'Brien, E.M., Sinclair, F.L., 2002. Sclerocarya birrea: A Monograph. School of Agricultural and Forest Sciences. University of Wales, Bangor, UK.
- Helm, C.V., Witkowski, E.T.F., 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. For. Ecol. Manag. 263, 175–188. http://dx.doi.org/10.1016/j.foreco.2011.09.024.
- Helm, C.V., Witkowski, E.T.F., 2013. Continuing decline of a keystone tree species in the Kruger National Park. South Africa. Afr. J. Ecol. 51 (2), 270–279. http://dx.doi.org/ 10.1111/aje.12032.
- Helm, C.V., Scott, S.L., Witkowski, E.T.F., 2011. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. S. Afr. J. Bot. 77 (3), 650–664. http://dx.doi.org/10.1016/j.sajb.2011.02.003.
- Hemborg, Å.M., Bond, W.J., 2007. Do browsing elephants damage female trees more? Afr. J. Ecol. 45 (1), 41–48. http://dx.doi.org/10.1111/j.1365-2028.2006.00666.x.
- Henley, M.D., 2013. Vegetation and Questionnaire Report. Unpublished report to the Associated Private Nature Reserves. Hoedspruit, South Africa.
- Hepburn, H.R., Kipyatkov, V.E., 2006. Absconding, migration and swarming in honeybees: an ecological and evolutionary perspective. In: Life Cycles in Social Insects: Behaviour, Ecology and Evolution. St. Petersburg University Press, St. Petersburg, Rus, pp. 121–135.
- Jacobs, O.S., Biggs, R., 2002. The impact of African elephant on marula trees in the Kruger National Park. S. Afr. J. Wildl. Res. 32 (1), 13–22 10520/EJC117144.
- Jacobson, E.R., Sundberg, J.P., Gaskin, J.M., Kollias, G.V., O'Banion, M.K., 1986. Cutaneous papillomas associated with a herpesvirus-like infection in a herd of captive African elephants. J. Am. Vet. Med. Assoc. 189 (9), 1075–1078.
- Karidozo, M., Osborn, F.V., 2005. Can bees deter elephants from raiding crops? An experiment in the communal lands of Zimbabwe. Pachyderm 39, 26–32.
- King, L.E., Douglas-Hamilton, I., Vollrath, F., 2007. African elephants run from the sound of disturbed bees. Curr. Biol. 17 (19), R832–R833. http://dx.doi.org/10.1016/j.cub. 2007.07.038.
- King, L.E., Douglas-Hamilton, I., Vollrath, F., 2011. Beehive fences as effective deterrents for crop raiding elephants: field trials in northern Kenya. Afr. J. Ecol. 49 (4), 431–439. http://dx.doi.org/10.1111/j.1365-2028.2011.01275.x.
- King, L.E., Lala, F., Nzumu, H., Mwambingu, E., Douglas-Hamilton, I., 2017. Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. Conserv. Biol. http://dx.doi.org/10.1111/cobi.12898.
- Laws, F.M., 1970. Biology of African elephants. Sci. Prog. 58 (230), 251–262. (1933-). http://www.jstor.org/stable/43419958.
- Mangiafico, S.S., 2015. An R Companion for the Handbook of Biological Statistics, Version 1.3.0. rcompanion.org/rcompanion.
- Midgley, J.J., Balfour, D., Kerley, G.I.H., 2005. Why do elephants damage savanna trees? Commentary. S. Afr. J. Sci. 101 (5/6), 213–215. http://dx.doi.org/10.520/ EJC96413.
- Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, South Africa.
- Ngama, S., Korte, L., Bindelle, J., Vermeulen, C., Poulsen, J.R., 2016. How bees deter elephants: beehive trials with forest elephants (*Loxodonta africana cyclotis*) in Gabon. PLoS One 11 (5), e0155690. http://dx.doi.org/10.1371/journal.pone.0155690.

- Nouvian, M., Reinhard, J., Giufra, M., 2016. The defensive response of the honeybee Apis mellifera. J. Exp. Biol. 219 (22), 3505–3517. http://dx.doi.org/10.1242/jeb.143016.
- Peel, M., 2015. Ecological Monitoring: Association of Private Nature Reserves (Timbavati, Umbabat, Klaserie and Balule). Unpublished Report to the Associated Private Nature Reserves, Nelspruit, South Africa.
- Poole, J.H., Moss, C.J., 1981. Musth in the African elephant, Loxodonta africana. Nature 292 (5826), 830–831. http://dx.doi.org/10.1038/292830a0.
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna (ISBN 3-900051-07-0 (cited 18 October 2016). Available from). http://www.Rproject.org.
- SANParks, 2012. Elephant management plan. Kruger National Park. 2013–2022. SANParks, Skukuza, South Africa.
- Shackleton, S.E., Shackleton, C.M., Cunningham, T., Lombard, C., Sullivan, C.A., Netshiluvhi, T.R., 2002. Knowledge on *Sclerocarya birrea* subsp. *caffra* with emphasis on its importance as a non-timber forest product in South and Southern Arica: a summary: part 1: taxonomy, ecology and role in rural livelihoods. South. Afr. For. J. 194 (1), 27–41. http://dx.doi.org/10.520/EJC33893.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R., Slotow, R., 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. J. Trop. Ecol. 24 (3), 281–289. http://dx.doi.org/10.1017/S0266467408004951.
- Smit, I.P.J., Grant, C.C., Whyte, I.J., 2007. Elephants and water provision: what are the management links. Divers. Distrib. 13 (6), 666–669. http://dx.doi.org/10.1111/j. 1472-4642.2007.00403.x.
- Vogel, S.M., Henley, M.D., Rode, S.C., Vyver, D., Meares, K.F., Simmons, G., Boer, W.F., 2014. Elephant (*Loxodonta africana*) impact on trees used by nesting vultures and raptors in South Africa. Afr. J. Ecol. 52 (4), 458–465. http://dx.doi.org/10.1111/aje. 12140.
- Vollrath, F., Douglas-Hamilton, I., 2002. African bees to control African elephants. Naturwissenschaften 89 (11), 508–511. http://dx.doi.org/10.1007/s00114-002-0375-2.
- Walker, B.H., Stone, L., Henderson, L., Vernede, M., 1986. Size structure analysis of the dominant trees in a South African savanna. S. Afr. J. Bot. 52 (5), 397–402. http://dx. doi.org/10.1016/S0254-6299(16)31502-2.