Elephant impact on marula trees, and African honeybees as a mitigation method

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Declaration

I declare that this Dissertation is my own work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted by me before for any other degree, diploma or examination at any other University or tertiary institution.

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Abstract

Concerns exist over the continual decline of marula trees (*Sclerocarya birrea* subsp. *caffra*) as a result of African elephant (*Loxodonta africana*) impact and a lack of recruitment and regeneration. One strategy of protecting adult marula trees is the usage of elephant mitigation methods. This study took place in Jejane Private Nature Reserve (JPNR), a protected area which recently opened up to the Greater Kruger National Park and had not had elephants in over 100 years. The aim of the study was to investigate the changes to the marula population structure in JPNR three years after the migration of elephants to the area due to fence removal, and to test whether African honeybees (*Apis mellifera* subsp. *scutellata*) could be used as a mitigation method for elephant impact on marula trees.

A previous size-class survey had been done on a sample of JPNR's marula population in 2009, prior to the fence removal in 2013. A resurvey of these trees was used to assess the elephant-induced impact and mortality levels on the marula trees and to compare these levels to previously recorded impact and mortality levels on marula trees in the Kruger National Park (KNP). Marula seed predation levels and seedling recruitment were also assessed to address recruitment concerns. The resurveyed marula population had declined by 23.8% post-elephant migration, with the highest annual mortality rates (AMR) and impact scores recorded for trees in the 5 - 11 m height classes. Impact scores on marula trees in JPNR were higher than impact scores recorded on KNP marula trees. Only two marula seedlings were found across all transects, with evidence of high seed predation on marula endocarps. JPNR displayed an adult-dominated marula population with a lack of regeneration, possibly due to a lack of fire which has increased available shelter for seed predators such as small mammals.

African honeybees were then used to investigate their effectiveness as an elephant mitigation method and to compare this method against wire-netting (a method experimentally used to prevent ring-barking by elephants). Fifty active beehives were hung from 50 marula trees, with another 50 dummy (inactive) beehives hung from branches on the opposite ends of each beehive tree's main stem. Fifty additional marula trees were wire-netted and a further 50 were used as control trees. Elephant impact on all 150 trees was measured prior to the addition of treatments and post-treatment addition for nine 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 marula trees against bark-stripping, but did not prevent elephants from breaking branches. Beehives proved highly efficient at mitigating all forms of elephant impact. The financial cost and maintenance required for the beehive mitigation method is greater than that of wire-netting, but the beehives can provide honey and pollination services as an additional benefit. The results of this study illustrate that African honeybees can be used as an effective non-lethal mitigation method for elephant impact on marula trees and are a viable strategy to reduce human-elephant conflict in South Africa's protected areas.

Keywords: *Apis mellifera* subsp. *scutellata*, beehive, control trees, Kruger National Park, *Loxodonta africana*, mitigation methods, mortality rates, regeneration, *Sclerocarya birrea* subsp. *caffra*, wire-netting

List of terms and abbreviations

AMR	Annual mortality rate (number of individual trees killed per year)
APNR	Associated Private Nature Reserves; collection of private nature reserves on the western boundary of the Kruger National Park, including the Balule, Klaserie, Timbavati and Umbabat Private Nature Reserves
BSD	Basal stem diameter; diameter of the main stem 30 cm above the ground
DBH	Diameter (of main stem) at breast height
DEA	Department of Environmental Affairs (South Africa)
Greater KNP	Greater Kruger National Park; expansive conservation area including the Kruger National Park and adjoining South African state and private nature reserves
JPNR	Jejane Private Nature Reserve; private nature reserve recently adjoined to the Greater KNP
HEC	Human-elephant conflict
Plantex glue	Glue substance used to protect resources against invertebrate pests
SANParks	South African National Parks
Shareholders	Private persons/families owning residency shares in Jejane Private Nature Reserve
Waksol	Wood preservative used for protecting exterior wooden surfaces

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Chapter 4: Synthesis and discussion

Chapter 1

General introduction

Rationale

Research problem

African elephants (*Loxodonta africana*) are described as major drivers of ecosystem change due to their ability to alter the environment through pushing down trees and opening up densely vegetated habitats (Coetzee *et al*. 1979; Calenge *et al*. 2002; Gadd 2002; Jacobs and Biggs 2002). In South Africa, concerns have been raised, however, over the impact of the high population densities of elephants on vegetation structure and diversity (Whyte *et al*. 1998; Owen-Smith *et al*. 2006). In particular, long-term studies on the effects of elephants on marula (*Sclerocarya birrea* (A. Richard) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae)) in the Greater Kruger National Park (Greater KNP) have reported severe elephant-related impact to adult trees through ring-barking, stem snapping and toppling events (Jacobs and Biggs 2002; Shannon *et al*. 2008; Helm and Witkowski 2012). Research has also found that there is a lack of marula recruitment in certain areas across southern Africa's savannas (Mosugelo *et al*. 2002; Helm and Witkowski 2012), with a scarcity of seedlings as a consequence of seed predation (Helm *et al*. 2011a), herbivory (Moe *et al*. 2009) and fire (Jacobs and Biggs 2001). These studies indicate that the loss of marula trees in protected areas is a more complex subject than solely elephant impact. However, as large marula trees are important for economic (Shackleton and Shackleton 2005) and aesthetic (Edge *et al*. 2017) purposes, as well as for providing valuable seed banks for the population (Helm *et al*. 2011a), it is important to develop methods which can mitigate elephant impact on these adult trees.

Motivation for study

Jejane Private Nature Reserve (JPNR), the study site of this research, is a protected area that has recently been opened up to the Greater KNP (Thomson 2013). Elephants had not been present in the JPNR area in over 100 years (G. Thomson, personal communication, November 23, 2016), and prior to the migration of elephants from the Greater KNP, JPNR had the highest adult marula tree density in the area (Helm and Witkowski 2012). Helm and Witkowski (2012) also recorded an adult-dominated marula population in JPNR prior to the migration of elephants due to fence removal, with high marula seed predation rates (Helm *et al*. 2011a). Following the migration of elephants into JPNR in 2013, shareholders within the protected area have expressed concerns over the impact that elephant have had on the local marula population (Weber 2014). The impact on adult marula trees is further exemplified by the lack of seedling regeneration within the JPNR marula tree population, as a possible consequence of high seedling predation by mesoherbivores. Therefore, by assessing the JPNR marula population three years post-elephant migration into JPNR, this study will be able to investigate: (1) the changes in the JPNR marula population structure and recruitment concerns, and (2) the usage of African honeybees (*Apis mellifera* subsp. *scutellata*) and beehives as a novel mitigation method to protect adult marula trees from elephant impact. The African honeybee is a notoriously aggressive honeybee species that swarms and attacks in large numbers when its beehive is disturbed (Wilson 1971; Alaux *et al*. 2009). In Kenya, research has shown that elephants actively avoid contact with swarms of African honeybees, avoiding trees with live beehives (Vollrath and Douglas-Hamilton 2002), crop fields surrounded by beehive fence-lines (King *et al*. 2009; 2011; 2017) and even moving away from the playback recordings of swarming honeybees (King *et al*. 2007). These findings offer the opportunity to explore the effectiveness of using active beehives as a non-lethal mitigation method to minimise elephant impact on adult marula trees in the Greater KNP in South Africa. Furthermore, the current South Africa Elephant Research Strategy (2013 - 2023) is focused on altering elephants' spatial and temporal access to resources (Ferreira *et al*. 2012; DEA 2013). Beehives may therefore provide South African conservation managers with a novel non-lethal mitigation method that will support this strategy.

Study aim and objectives

This study aims to investigate the changes to the marula population structure in Jejane Private Nature Reserve since the migration of African elephants due to fence removal, and to test whether African honeybees can be used as a mitigation method for elephant impact on marula trees.

Chapter 2 objectives

Objective 1 Assess the elephant-induced impact and mortality levels on the previously surveyed JPNR marula population.

Objective 2 Compare these levels to previously recorded impact and mortality levels on marula trees in central and southern KNP.

Objective 3 Assess marula seed predation and seedling recruitment to address marula regeneration in JPNR.

Chapter 3 objectives

Objective 1 Test whether the presence of beehives in marula trees influenced the likelihood of the tree receiving elephant impact and compare these results to wire-netted trees (a method experimentally used to prevent ring-barking by elephants).

Objective 2 Assess if elephants avoided areas with marula trees containing beehives.

Objective 3 Provide a comparison of the financial costs associated with the beehive and wire-netting mitigation methods.

Literature Review

Elephant impacts on large trees

Ecosystem engineers

African elephants are considered to be one of the major drivers of ecosystem functioning by altering landscapes, promoting landscape patchiness, and increasing the nutrients available to the soil (Anderson and Coe 1974; Dublin *et al*. 1990; Coverdale *et al*. 2016). Elephants are subsequently termed ecosystem engineers, since the presence or absence of their interactions within an ecosystem can alter the system's species composition and structure (Jones *et al*. 1994). Elephants provide a number of ecosystem benefits including the dispersal of seeds (Chapman *et al*. 1992; Cochrane 2003; Bunney *et al*. 2017), the removal of dense vegetation to create a heterogeneous landscape (Owen-Smith 1988; Grainger *et al*. 2005; White and Goodman 2010) and the cycling of nutrients (Anderson and Coe 1974; Augustine and McNaughton 1998). Indirectly, elephants can also facilitate small mammalian herbivores by felling large trees which enable small herbivores to feed on browse material that would otherwise be unattainable (Jachmann and Bell 1985; Fritz *et al*. 2002; Makhabu *et al*. 2006). However, concerns have been raised over the negative impacts brought about by high densities of elephants in enclosed reserves and the implications of these impacts on biodiversity preservation (Western 1989; Cumming *et al*. 1997; Western and Waitumo 2004). By altering landscapes and creating landscape patchiness, elephants have the ability to affect species composition by changing the availability of food sources and habitat for other species (Owen-Smith 1988). In Sweetwaters Game Reserve, Kenya, an increase in elephant numbers has been correlated with a decrease in habitat suitability for the black rhinoceros (*Diceros bicornis*), therefore leading to a decrease in black rhinoceros breeding success (Birkett 2002). Furthermore, it is hypothesised that elephants may directly compete with kudu (*Tragelaphus strepsiceros*) for browse vegetation, thereby placing pressure on kudu population in enclosed protected areas (Kerley and Landman 2006). However, Skarpe *et al*. (2004) recorded that increasing elephant numbers in Chobe National Park, Botswana, had no negative influence on the population numbers of impala (*Aepyceros melampus*) and buffalo (*Syncerus caffer*). These studies further add to the complexity of how elephants both positively and negatively affect the species composition of other herbivores, both through facilitation and competition (Owen-Smith 1988).

Three factors have been proposed to explain the causation of woodland conversion by elephants. The first factor correlates high elephant densities with a loss of woodland habitat (Lewis 1987; Western 1989; Dublin *et al*. 1990). High elephant densities in small, compressed protected areas could lead to longer and more frequent encounter rates between elephants and specific woodland habitat, thereby increasing impact levels at a higher rate than in larger protected areas (O'Connor *et al*. 2007). The second factor relates to the high nutritional and energetic requirements of elephants as a consequence of their large body size and therefore, the pressure they exert on the environment to obtain these energy requirements (Clemens and Maloiy 1982; Zyambo 2016). The third factor describes the seasonal variation in elephant diet from a predominantly grazing-based diet in the wet season to a browsing-based diet in the dry season (Bell 1985; Owen-Smith 1988; Codron *et al*. 2006). This variation is further exemplified during a drought when elephants become increasingly reliant on woody vegetation to fulfil their nutritional requirements (Van de Vijver *et al*. 1999; Styles and Skinner 2000). Long-term studies have reported significant declines in large tree densities in South Africa's protected areas and how the loss of large trees could affect ecosystem functioning (Viljoen 1988; Trollope *et al*. 1998; Whyte *et al*. 2003; Asner *et al*. 2015). Large trees are important for ecosystem services as they provide both foraging opportunities and habitat for numerous species (Du Toit 1990; Hall *et al*. 2002; Shackleton *et al*. 2002; Vogel *et al*. 2014), as well as being important for the cycling of nutrients (Scholes and Archer 1997). Concerns currently exist over the potential loss of species diversity where large trees are heavily impacted by elephants (Herremans *et al*. 1995; Cumming *et al*. 1997), as well as the removal of keystone tree species (Edkins *et al*. 2008; Helm *et al*. 2009; Helm and Witkowski 2013). Elephants impact trees in numerous ways including debarking, branch breakage, snapping of main stems (also known as pollarding; O'Connor *et al*. 2007), or uprooting entire trees (Coetzee *et al*. 1979; Calenge *et al*. 2002; Shannon *et al*. 2008; Helm *et al*. 2009; Ihwagi *et al*. 2012). Once impacted, certain species of trees are able to coppice or self-heal (Coetzee *et al*. 1979; Shackleton 2001). However, the decrease in height after being impacted by elephants makes these individuals vulnerable to the effects of fire (Jacobs and Biggs 2001). Bark-stripping for example, removes phloem and cambium from the tree, which can lead to eventual root death (Michaletz and Johnson 2007), invasion by termites and woodborers (Hatcher 1995), or increased vulnerability to fire (Moncrieff *et al*. 2008). A variety of hypotheses have been formulated to explain the possible motivations or reasons behind elephant impact on large trees. The non-adaptive hypotheses describe elephant feeding behaviour as being simply over-robust or destructive (Russell 1968; Stokke and du Doit 2000), with elephants breaking large branches or pushing over trees to access the out-of-reach leaves and branches (Styles and Skinner 2000). The sexual and social hypotheses describe elephant impact on large trees being associated with the activities of ´confidence building' and muscular training, especially in bulls (Croze 1974; Guy 1976; Midgley *et al*. 2005). The sexual and social hypotheses offer an explanation as to why elephant impact can be observed on non- forage species such as milkwood (*Sideroxylon inerme*

L.) and tamboti (*Spirostachys africana* Sond.) (Midgley *et al*. 2005). Research has further shown that levels of tree impact can differ between tree species based on elephants' selectivity preferences (Ihwagi *et al*. 2012), with studies finding marula trees to be a preferred forage choice for elephants (Weaver 1995; Greyling 2004, Shannon *et al*. 2008; Henley 2013).

Elephant impact on marula trees (Sclerocarya birrea subsp. *caffra*)

Elephant impact on marula trees has been studied extensively because of the cultural, ecological and economic importance of the tree species (Shackleton *et al*. 2002). Severe bark stripping has been recorded on the marula population within the Greater KNP (Coetzee *et al*. 1979; Owen-Smith 1988; Helm *et al*. 2009; Helm and Witkowski 2013), with branch breakage being another common form of elephant impact (Gadd 2002; Jacobs and Biggs 2002). Extreme herbivory such as main stem snapping and toppling has been recorded for trees greater than 2.5 m in height (Jachmann and Bell 1985; Jachmann and Croes 1991; Helm *et al*. 2009).

The preferred browsing height of African elephants is 2 - 3 m (Jachmann and Croes 1991), although more severe impact is observed on trees over 5 m in height as these trees are pushed over and fed on by adult elephants (Coetzee *et al*. 1979; Jacobs and Biggs 2002; Helm *et al*. 2009; Helm and Witkowski 2013). Most of the more extreme impact is caused by elephant bulls (Greyling 2004, Helm and Witkowski 2012). There are also differences in the levels of impact recorded on male and female marula trees (Hemborg and Bond 2007). One of the attractants of marula trees for elephants is the fruit, which are only found on female trees (Shackleton *et al*. 2002). The presence of these fruits may therefore lead to greater impact on the female trees as the elephants may be specifically selecting for trees with fruit (Hemborg and Bond 2007; Helm *et al*. 2009). Differences in elephant impact between male and female marula trees, however, may not always be visible (Gadd 2002), especially during non-fruiting periods. Studies have found a bias in the male-to-female sex ratio, with more male marula trees present in comparison to female marula trees (Helm *et al*. 2009; Henley 2013). The skewed sex ratio does indicate possible increased elephant utilisation of female marula trees, although this may also be a result of high pollen availability but a lack of pollinator success (Hall *et al*. 2002). This issue requires further research into the distribution and abundance of African honeybees, as honeybees, along with flies and wasps, are the major pollinators of marula trees (Hall *et al*. 2002; Chirwa and Akinnifesi 2008).

A marula tree's distance from a road can also influence its probability of being impacted by elephants. Elephant bulls regularly follow roads, making trees alongside these roads more vulnerable to impact than those further away (Pienaar 1968). In a detailed study on road effects, it was found that marula were heavily impacted within 10 m of a road; intermediately impacted between 10 - 50 m; and there was relatively little impact on trees over 50 m from a road (Coetzee *et al*. 1979). Although no road effect was observed in a study preformed in the private reserves of the Greater KNP (Gadd 2002), it is important to acknowledge the effect that roads may have on marula trees' susceptibility to impact.

Understanding the effects of elephant impact on marula trees is more complicated than simply assessing impact levels. When bark is removed, a narrow strip of bark is enough to keep a marula tree alive, after which fresh bark is slowly produced (Coetzee *et al*. 1979; Lewis 1987). Scars however remain and may leave the tree more vulnerable to further impact (Coetzee *et al*. 1979). Marula trees that have been uprooted or stem snapped are also capable of coppicing or resprouting (Coetzee *et al*. 1979; Haig 1999; Gadd 2002). Scogings *et al*. (2012) have even demonstrated that marula trees respond to herbivory by growing longer shoots (compensatory growth) with an increase in the number of leaflets per surface area, as well as by increasing the surface leaf area of these new leaflets. Although marula trees can survive elephant herbivory, the smaller coppicing stems become more vulnerable to fire, and in protected areas that implement fire management regimes, these trees may not be able to escape the fire trap and are consequently killed by intense fires (Jachmann and Croes 1991; Jacobs and Biggs 2001; Helm *et al*. 2009; Helm *et al*. 2011b; Midgley *et al*. 2012; Henley 2013). Therefore, although elephants may rarely directly kill a large percentage of marula trees, they have an indirect impact on a far greater percentage of trees through these additional effects (Jacobs and Biggs 2001; Gadd 2002).

The loss of marula trees, however, is not only due to high elephant densities in protected areas. External factors affecting marula recruitment at both the seed and seedling life stages increases the survival pressures on marula populations.

Marula regeneration and recruitment

Marula seed dispersal

The persistence of marula populations is regulated by the recruitment and regeneration rate of seeds into seedlings and seedlings into adult trees, as well as the mortality rates at all of these life stages (O'Connor *et al*. 2007). Seed dispersal mechanisms determine the distribution and clumping of species (Nathan and Muller-Landau 2000). In what is termed a 'seed shadow', high densities of seeds are usually found underneath or in close proximity to the parent tree, decreasing in density further away (Wilson 1993). Both biotic and abiotic processes are responsible for the movement of seeds away from their parent trees and can ultimately influence the 'seed shadow' distribution pattern of a particular tree species (Schupp and Fuentes 1995; Wilson and Traveset 2000).

Only female marula trees produce sweet fleshy fruits, which may contain 0 - 4 seeds per fruit (Coates Palgrave 1993; Shackleton *et al*. 2002; Leakey *et al*. 2005). The seeds are stored inside a strongly lignified endocarp, where each seed has its own locule and is enclosed by an individual operculum (Shackleton *et al*. 2002; Midgley *et al*. 2012). Marula seeds are diplochorous, in that they have two different dispersal distances or methods: primary and secondary dispersal (Vander Wall and Longland 2004). Both of these dispersal methods can result in either germination or seed predation (Helm *et al*. 2011a). Primary dispersal occurs when the marula fruit is dropped directly from the tree's canopy onto the ground (Helm *et al*. 2011a). A certain degree of dormancy then occurs as the strong endocarp casing prevents oxygen from reaching the seeds, thereby hindering seed germination (Schopfer *et al*. 2001). During their assessment of marula endocarp densities around the canopy of female marula trees, Helm *et al*. (2011a) found the highest density of endocarps in the inner canopy (trunk to 1/2 radius), after which the endocarp density decreased with an increased distance from the parent tree.

Secondary dispersal occurs when marula endocarps from underneath the canopy or on the tree itself are dispersed by dispersal agents (Helm *et al*. 2011a; Bunney *et al*. 2017). Secondary dispersal agents include African elephant, vervet monkey (*Cercopithecus aethiops*), chacma baboon (*Papio ursinus*), kudu (*Tragelaphus strepsiceros*), savanna tree squirrel (*Paraxerus cepapi*), white rhino (*Ceratherium simum*), reedbuck (*Redunca* subsp.) and warthog (*Phacochoerus aethiopicus*) (Palmer and Pitman 1972; Estes 1991; Helm *et al*. 2011a; Bunney *et al*. 2017). African elephants are one of the most important secondary dispersal agents of marula seeds, as their digestive tract juices alter the operculum properties and increase the rate of germination (Lewis 1987). Elephants also transport marula endocarps away from the parent tree, reducing intraspecific competition amongst emerging seedlings in the process (Midgley *et al*. 2012; Bunney *et al*. 2017). However, rodents are also classified as important secondary dispersal agents of marula seeds (Midgley *et al*. 2012). The dispersal distances by rodents are shorter than those of elephants, reaching on average 20 m away from the parent tree (Takahashi *et al*. 2007). However, by burying the marula endocarps underneath the ground, the seeds are protected against both predation and fire, thereby allowing them to successfully germinate after the following rain season (Midgley *et al*. 2012). Although marula seeds have a variety of secondary dispersal agents, many seeds are still predated on either before or during the dispersal of the endocarp (Midgley *et al*. 2012), reducing the number of viable seeds that may germinate into seedlings (Crawley 1989).

Marula seed predation

Seed predation is a form of herbivory which is often overlooked, but can play a distinctive role in plant population growth rate (Babweteera *et al*. 2007; Kurkjian *et al*. 2016). Although plants are expected to produce more seeds than what would naturally germinate (Crawley 1989), high levels of seed predation can have a negative influence on the growth rate of a particular species (Maron and Crone 2006; Kurkjian *et al*. 2016). Seeds which fall onto the soil surface are subject to high rates of seed predation from birds, insects, and rodents (Hulme 1998; Kolb *et al*. 2007; Bricker and Maron 2012). Some seeds are able to escape this predation through abiotic burial into the soil (Chambers *et al*. 1991). Abiotic burial however, is reliant on both the seeds' and soils' characteristics (Chambers *et al*. 1991; Thompson *et al*. 2000). It is especially difficult for large seeds, or seeds within large endocarps or casings, to enter the soil (Thompson *et al*. 2000). Seeds exposed on the soil surface are therefore vulnerable to seed predators (Reader 1991).

Seed predation on marula seeds is a common seed fate that occurs once either primary or secondary seed dispersal has taken place (Helm *et al*. 2011a; Midgley *et al*. 2012). Parrots, rodents, as well as other small mammals have been recorded predating marula seeds by manually opening the marula endocarps (Palmer and Pitman 1972; Manson *et al*. 2001; Symes and Perrin 2003; Goheen *et al*. 2004). The savanna tree squirrel (*Paraxerus cepapi*) is one of the key predators of marula seeds within the Greater KNP, feeding off seeds from both underneath adult trees, as well as within elephant dung (Pienaar 1968; Helm *et al*. 2011a; Midgley *et al*. 2012). The most common technique of seed predation by squirrels is to manually remove the marula endocarp's operculum and feed on the seed within the locule (Midgley *et al*. 2012). Another mode of entry is through the side of the marula endocarp (Midgley *et al*. 2012). An open locule is therefore indicative of possible seed predation (Helm *et al*. 2011a; Midgley *et al*. 2012). Helm *et al*. (2011a) recorded varying seed predation levels of 19 - 74% across different sites within the Greater KNP. Sites experiencing high levels of seed predation were associated with low fire regimes (Helm *et al*. 2011a), which may increase vegetation cover and therefore, rodent numbers (Reader 1991; Kurkjian *et al*. 2016). High levels of seed predation can result in a bottleneck effect for marula populations within these protected areas, as seed limitation becomes an important factor influencing the number of new seedlings and ultimately, adult marula trees within a population (Helm *et al*. 2011a; Kurkjian *et al*. 2016).

Marula seedling establishment

Seeds that germinate into seedlings are under new selective pressures which are often amplified by artificial management in protected areas (Moles and Westoby 2004). Changes from woodland cover to shrubland have been reported across southern Africa, largely due to a lack of seedling establishment of large tree species (Mosugelo *et al*. 2002; Skarpe *et al*. 2004; Rutina *et al*. 2005; Babweteera *et al*. 2007; Moe *et al*. 2009). Seedling establishment can be affected by a variety of factors such as seed limitation (Eriksson and Ehrlen 1992), climate influence (Asner and Levick 2012), fire intensity (Trollope 1983), trampling by megafauna (Lawes and Chapman 2006), as well as herbivory (Lewis 1987). Tree species that have episodic recruitment strategies such as marula and baobab (*Adansonia digitata* L.) are most at risk if the above mentioned factors prevent the majority of seedlings within a population from establishing into adults (O'Connor *et al*. 2007; Helm *et al*. 2011a; Venter and Witkowski 2013; Taylor 2016).

Fire management practices have been regarded as one of the major threats to the survival rate of the seedlings of large trees in South Africa, with seedlings under 0.5 m in height being most vulnerable to intense fires (Trollope 1983; Zyambo *et al*. 2016). The fire threshold of marula seedlings is even greater, with seedlings under 1.5 m in height being most at risk from fire management practices (Jacobs and Biggs 2001). The previous burning policy of the KNP is considered to be a major factor that has impeded the establishment of marula seedlings (Jacobs and Biggs 2001; Helm *et al*. 2009). Studies have also indicated that a decrease in marula seedling survival is correlated with increased impala (*Aepyceros melampus*) densities (Lewis 1987; Gadd 1997; Haig 1999; Kauffman and Maron 2006; Helm and Witkowski 2012). Impala are seedling browsers (Lewis 1987) and marula seedlings are highly palatable (Walker *et al*. 1986). In the northern regions of Chobe National Park, the decline of woodland vegetation has been largely attributed to the browsing pressure of increasing impala densities (Mosugelo *et al*. 2002; Skarpe *et al*. 2004; Moe *et al*. 2009). In some areas of the Greater KNP, there is evidence that lower impala densities are correlated with increased marula seedling survival rates (Helm and Witkowski 2012). There is also evidence that other seedling browsers such as giraffe (*Giraffa camelopardalis*) may have a significant impact on marula seedling survival (Pellew 1983). Trampling by megafaunal species is another threat facing marula seedlings. Female adult marula trees offer both shade and fruit for megafaunal species (Helm *et al*. 2011a). Furthermore, the majority of potential marula seedlings are found underneath the adult tree's canopy, especially in areas where seed dispersal agents may be limited (Helm *et al*. 2011a; Midgley *et al*. 2012). A high possibility therefore exists that marula seedlings underneath adult trees may be trampled by megafaunal species seeking shade or fruit (Helm *et al*. 2011a; Lawes and Chapman 2006), particularly in protected areas where elephant-marula tree encounter rates are high (O’Connor *et al*. 2007).

The marula tree has been listed as a protected species in South Africa since 1962 (Hall 2002; Shackleton and Shackleton 2005) and therefore, conservation managers have attempted various methods at protecting this tree species. Although a variety of environmental factors affect the marula population at each life stage (as described above), primary managerial efforts have focused on mitigating elephant impact on adult trees.

Elephant impact mitigation

Overview

The destructive nature of elephant foraging has often resulted in conservationists attempting to understand and control the effects that elephants have on vegetation (Caughley 1976; Grant *et al*. 2008; Kerley *et al*. 2008). Elephant impact on vegetation in South Africa’s protected areas was often managed by controlling elephant numbers as a means of reducing the effects of high densities of elephants (Whyte *et al*. 1998; Whyte *et al*. 2003). From 1966 - 1994, South Africa’s Kruger National Park (KNP) carried out annual culling operations where the elephant population was maintained at 7,000 - 8,500 individuals (Whyte *et al*. 1998). There has been a scientific paradigm shift however, coupled with social and political pressures, in that elephant impacts on the environment should be controlled by managing and manipulating elephant effects rather than elephant numbers alone (Owen-Smith *et al*. 2006; Ferreira *et al*. 2012; DEA 2013). In attempts to minimise elephant effects on particular natural and artificial structures, mitigation methods have been developed in an attempt to alter elephant behaviours and impacts. Within the Greater KNP for example, the adaptive elephant management plan includes the closure of manmade surface water bodies, fenced-off enclosures, electrified fencing, pepper fires, acoustic playbacks, as well as disturbance shooting (SANParks 2012). Other elephant mitigation methods which have been used elsewhere in Africa include chili extracts (Parker and Osborn 2006), stone walls (Omondi *et al*. 2004), as well as flares and fireworks (Hoare 2001). Most of these mitigation methods focus on keeping elephants away from resources within specific areas. Further mitigation methods have been developed to operate on a localised-scale at mitigating elephant impact on specific vegetation (e.g. large trees). These include wire-netting (Henley 2013; Derham *et al*. 2016) and African honeybees (Vollrath and Douglas-Hamilton 2002).

Wire-netting as a means of mitigating elephant impact on large trees

The use of wire netting as a non-lethal method to mitigate elephant effects on large trees has been carried out in Kenya's Samburu National Reserve (Gordon 2003) and in the Associated Private Nature Reserves (APNR) in the Greater KNP (Henley 2013; Derham *et al*. 2016). Wire-netting trees does not result in the total avoidance of these trees by elephants, but has been highly successful at preventing bark-stripping and eventual ring-barking of trees (Henley 2013; Derham *et al*. 2016). To wire-net a tree, 1.8 m of 13 mm chicken-mesh is wrapped around the trunk of a mature tree, 50 cm from the ground (Henley 2013). The wire-netting method has proven successful at improving the survival rates of trees in the Greater KNP (Henley 2013). The most common form of elephant impact on wire-netted trees is primary branch breakage, with main stem breakage and uprooting also recorded on wire-netted trees (Grant *et al*. 2008; Henley 2013). It is however, a relatively cost-effective mitigation method that requires very little maintenance, making it advisable for large-scale usage.

African honeybees as a means of mitigating elephant effects on vegetation

African honeybees were first used as a mitigation method to deter elephants from impacting *Vachellia xanthophloea* Benth. in Kenya (Vollrath and Douglas-Hamilton 2002), where both occupied and unoccupied beehives were hung from the trees at the eyelevel height of elephants (1.5 - 2 m). The occupied beehives provided full protection to the trees, and one third of the trees with unoccupied hives were left undamaged as well. In Zimbabwe, elephants also appeared to change their localised movement paths when confronted with the presence of beehives (Karidozo and Osborn 2005). It was hypothesised that there existed a negative association between the sound or smell of a beehive and the painful event of a bee-sting (Vollrath and Douglas-Hamilton 2002). African honeybees produce a continuous buzzing sound from the beehive as individuals fan their wings to lower the beehive's temperature (Gary 1992), and the honeybee beehives have mixtures of pheromones from sources such as wax, propolis, as well as from the honeybees themselves (Nouvian *et al*. 2016). Meanwhile, elephants have sensitive inner trunks and eyes, which could make them vulnerable to attacks from honeybees (Jacobson *et al*. 1986).

Playback recordings of the sounds of buzzing honeybees were used to investigate how elephants reacted to the sounds of aggravated honeybees (King *et al*. 2007). Elephants subjected to the buzzing sounds displayed alarm behaviours by ceasing their current activities, shaking their heads, smelling around themselves, producing distinct rumbling vocalisations and moving away from the sound in a bunched retreat (King *et al*. 2007). After recording the unique rumble vocalisations, the researchers played them back to elephant herds which had not been exposed to the original honeybee recordings (King *et al*. 2010). The alarm behaviours, previously observed in King *et al*. (2007), were displayed by the new elephant herd which had only been exposed to the rumble vocalisations. It therefore appears that this rumble sound emitted by elephants when in the presence of honeybee buzzing sounds is an evolved referential signal to the external threat of honeybees (King *et al*. 2010).

African honeybees have further been used to successfully deter elephants from crop raiding in Kenya (King *et al*. 2009; 2011; 2017). Beehive fence-lines have been designed to surround crop fields in an attempt to deter elephants from crop fields. The beehives (both occupied and unoccupied) are connected to one another by wires, meaning that any disturbance to the wires will disturb the beehives and result in the swarming of the honeybees (Wilson 1971). The honey harvested from the beehive fence-lines has also been used to bring in additional income into the villages (King *et al*. 2011; 2017).

Researchers have also found that the West African honeybee (*A. m.* subsp. *adansonii*) can effectively protect fruiting trees from impact by forest African elephants (*L. cyclotis*) (Ngama *et al*. 2016). By using the *Irvingia gabonensis* Baill. and *Sacoglottis gabonensis* Baill. fruiting trees, it was observed that the presence of beehives in these two tree species reduced the number of elephant visits to each tree, as well as the length of time spent in the vicinity of these beehive trees (Ngama *et al*. 2016). Active beehives also received fewer elephant visits in comparison to non-active beehives, and beehives with high honeybee activity levels received the least number of visits from elephants (Ngama *et al*. 2016). This was the first study to correlate beehive activity levels with elephant reactions to the beehives.

Research on elephant-honeybee interactions reveal the possibility of using honeybees as a mitigation method for elephant impact on tree species elsewhere. It is however, unknown as to whether or not any past associations exist between elephants and honeybees within protected areas in South Africa and how elephants will respond to the presence of beehives hanging in marula trees.

Study organisms

Sclerocarya birrea subsp. *caffra* (Marula)

The marula tree (family: Anacardiaceae) is a fast growing dioecious and deciduous tree, reaching heights of 7 - 17 m (Shackleton *et al*. 2002). The marula tree is often a community dominant and is a keystone species with both ecological and economical uses (Shackleton *et al*. 2002). It has a warm temperate to tropical distribution (Van Wyk 1974; Coetzee *et al*. 1979). Marula trees occur on a wide variety of soil-types, from deep sands on granite to plains of basalt, but are most commonly found on well-drained soil crests in regions with a mean annual rainfall of 200 - 1500 mm (Lewis 1987; Peters 1988). Although there are reported cases of marula trees being morphologically androdioecious (Diallo *et al*. 2006), it is the female trees that produce sweet fleshy fruits which can contain 0 - 4 seeds per fruit (Coates Palgrave 1993; Shackleton *et al*. 2002; Leakey *et al*. 2005). Important pollinators of marula trees include honeybees, wasps and flies (Chirwa and Akinnifesi 2008). Marula is an important ecological tree species, providing food for browsers and invertebrates (Palmer and Pitman 1972; Kroon 1999; Helm *et al*. 2009), as well as providing habitats for a number of small vertebrates, invertebrates, parasitic plants, sub-canopy grasses and forbs (Shackleton *et al*. 2002). Marula trees are also important on a cultural and commercial scale across southern Africa, which is one of the main reasons why it is spared by woodcutters in rural areas of southern Africa (Coates Palgrave 1993; Shackleton *et al*. 2002; Wynberg *et al*. 2002; Shackleton and Shackleton 2005).

Loxodonta africana (African elephant)

The African elephant (family: Elephantidae) is the world’s largest land mammal, distributed throughout southern, eastern and central Africa (Skinner and Chimimba 2005). African elephants live in a structured and complex society where males and females live in separate, but interrelated home ranges (Moss and Poole 1983; McComb *et al*. 2001; Archie *et al*. 2006). Cows spend their entire lives in matriarch-led family groups comprised of mother-offspring bonds (Moss and Poole 1983; Archie *et al*. 2006). Elephant bulls leave their natal family groups when they are around the age of fourteen years and proceed to associate with other bulls or live a relatively solitary lifestyle (Moss and Poole 1983). Elephants are non-territorial and have home ranges related to habitat productivity (Gaylard *et al*. 2003; Smit *et al*. 2007). They are mixed feeders, consuming large quantities of grass and browse (4 - 6% of their body weight daily), although specific grass-to-browse intake levels can vary across seasons (Laws 1970; Owen-Smith 1988; Codron *et al*. 2006). Elephants also regularly need to drink water and are therefore found where there is adequate surface water (Smit *et al*. 2007; Harris *et al*. 2008). Since culling was banned in South Africa's Greater KNP in 1994, the elephant population has increased from 7,806 individuals in 1994 to currently over 18,000 individuals (Whyte 2001; Chase *et al*. 2016). South Africa currently has the 6th largest elephant population in Africa (Chase *et al*. 2016).

Apis mellifera subsp. *scutellata* (African honeybee)

Apis mellifera subsp. *scutellata* is one of twenty four subspecies of *Apis mellifera* (Apidae) and is often referred to as the African honeybee (Ruttner 1988). African honeybees are distributed throughout southern and eastern Africa, found most commonly in woodland and grassland savannas (Ruttner 1988; Hepburn and Radloff 1998). There are three castes or types of African honeybees, each one distinguishable by their morphology and the activities they preform: queens, workers, and drones (Winston 1992; Hepburn and Radloff 1998). Each colony has one active queen that is responsible for laying eggs and is one-and-a-half times larger than the workers (Winston 1992). Workers, which are females with abnormally developed reproductive organs, are responsible for a number of duties including beehive maintenance, brood rearing, collecting pollen, as well as defending the colony against predators (Winston 1992; Human *et al*. 2006). Drones are males which have the sole responsibility of mating with the virgin queen (Winston 1992). African honeybees can forage between 400 - 1400 m from their beehives (Schneider 1989; Schneider and McNally 1993; Waddington *et al*. 1994), although foraging ranges of up to 6 km have been recorded (Visscher and Seeley 1982). In the wild, African honeybees may inhabit tree or earthen cavities, with water and resource availability being two major factors driving where colonies nest (Schneider and McNally 1993; McNally and Schneider 1996; Fleming *et al*. 2007). Water and resource availability is hypothesised to be one of the reasons as to why wild colonies may occur in clusters, with beehives usually separated by 100 - 200 m (Oldroyd *et al*. 1995; McNally and Schneider 1996).

Dissertation outline

This dissertation consists of two data chapters (Chapters 2 and 3), as well as an introduction chapter (Chapter 1) and a conclusion chapter (Chapter 4). Both data chapters have been written in the format of scientific papers and the repetition of information on certain aspects is unfortunately unavoidable in this format. The first chapter in this dissertation contains the rationale and motivation for the study, the aims and objectives of each data chapter (chapters 2 and 3), as well as a general introduction (literature review) on how elephants and other environmental factors affect marula population dynamics in protected areas, and the usage of wire-netting and African honeybees as elephant mitigation methods. Chapter 2 investigates the impact that elephants have had on Jejane Private Nature Reserve's marula population and if any marula recruitment is taking place. Chapter 3 investigates the usage of African honeybees as a mitigation method for elephant impact on marula trees and compares its effectiveness to wire-netting. Chapter 4 provides an overview of Chapters 2 and 3, and offers recommendations on the usage of African honeybees as a mitigation method for elephant impact on large trees. This chapter also suggests potential research avenues to be carried out on elephant-honeybee interactions.

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Chapter 2

Recent exposure to African elephants after a century of exclusion: rapid accumulation of marula tree impact and mortality, and poor regeneration

Abstract

Concerns exist over the continual decline of *Sclerocarya birrea* subsp. *caffra* (marula), a large ecologically and economically important tree species in southern Africa, primarily as a consequence of impact by African elephants (*Loxodonta africana*) and poor regeneration in some areas. I assessed changes in marula population structure in a reserve that was only recently opened to elephants. Jejane Private Nature Reserve (JPNR) has been subjected to elephants from the Greater Kruger National Park (Greater KNP) only since 2013, as it was fenced off beforehand. A previous survey of the marula population in JPNR was done in 2009 and again in 2016. Therefore this study aimed to (i) assess elephant-induced impact and mortality levels on the previously surveyed JPNR marula population, (ii) compare these levels to previously recorded impact and mortality levels on marula trees in central and southern KNP, and (iii) assess marula seed predation and seedling recruitment to address its regeneration. The resurveyed marula population had declined by 23.8% post-elephant migration due to fence removal, with the highest annual mortality rates (AMR) and elephant impact scores recorded for trees in the 5 - 11 m height classes. The JPNR marula tree AMR of 8.1% was higher than that of KNP (4.6%). Elephant impact scores on marula trees in JPNR were higher than impact scores recorded on KNP marula trees in both 2001 and 2008. Only two marula seedlings were found across all transects, whilst 84.2% of all endocarps' locules had seeds missing and bite marks were present on 42.3% of all endocarps. This indicates high levels of seed predation and a lack of seedling recruitment. JPNR displayed an adult-dominated marula population with an absence of juveniles. The concern over the impact by elephants on adult marula trees is therefore escalated as a consequence of the lack of recruitment and regeneration, primarily because of seed and seedling predation. Management policies should be focused on decreasing the water availability within JPNR to control elephant densities and impacts on large trees, as well as to focus on direct elephant mitigation methods for protecting large trees.

Keywords: Jejane, Kruger National Park, *Loxodonta africana*, mortality rates, regeneration, *Sclerocarya birrea* subsp. *caffra,* seed predation

Introduction

African elephants (*Loxodonta africana* Blumenbach 1797) are considered to be one of the major drivers of ecosystem functioning, owing to their ability to alter landscapes, promote habitat heterogeneity, and increase soil nutrient availability (Anderson and Coe 1974; Dublin *et al*. 1990; White and Goodman 2010; Coverdale *et al*. 2016). Elephants are consequently known as ecosystem engineers and keystone species, since their presence or absence within an ecosystem can alter the system's species composition and functioning (Jones *et al*. 1994). Elephants provide a number of ecosystem benefits, including the dispersal of seeds (Chapman *et al*. 1992; Cochrane 2003) with elephant bulls having the ability to disperse the seeds of megafaunal fruit such as marula (*Sclerocarya birrea* (A. Richard) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae)) up to 65 km with maximum gut passage time (Bunney *et al*. 2017). Elephants are also known to remove dense vegetation to create a heterogeneous landscape (Owen-Smith 1988; Grainger *et al*. 2005; White and Goodman 2010). However, concerns have been raised in South Africa over the potentially negative impacts that can result from high densities of elephants in enclosed reserves and the implications of these impacts on biodiversity preservation (Ben-Shahar 1998; Gandiwa *et al*. 2011; Asner *et al*. 2015). Long-term studies have reported a significant decline in large tree densities in South Africa's Kruger National Park (KNP) and how the loss of large trees could affect ecosystem functioning (Viljoen 1988; Trollope *et al*. 1998; Whyte *et al*. 2003; Asner *et al*. 2015). Large trees are important for ecosystem services, providing foraging opportunities and habitats for numerous species (Du Toit 1990; Hall *et al*. 2002; Shackleton *et al*. 2002; Vogel *et al*. 2014), as well as being critical for the cycling of nutrients (Scholes and Archer 1997). Large trees can receive impact by elephants in a variety of ways, including branch breakage, bark-stripping, main stem snapping and uprooting of entire individuals (Coetzee *et al*. 1979; Shannon *et al*. 2008; Helm *et al*. 2009). Elephants forage on branches and bark when the availability of green grass decreases (Styles and Skinner 2000), consuming large quantities of bark that has sugar-containing phloem tissue (Owen-Smith 1988). Although some trees are able to coppice or heal after elephant impact (Coetzee *et al*. 1979), the stunted growth can leave these trees vulnerable to the effects of fire (Jacobs and Biggs 2001), whilst debarking removes phloem and cambium, potentially leading to eventual root death (Michaletz and Johnson 2007) or the invasion of termites and woodborers (Hatcher 1995).

Extensive research has been focused on the impact that elephants have on marula trees, particularly because of the species' cultural, ecological and economic importance (Coetzee *et al*. 1979; Gadd 2002; Shackleton *et al*. 2002; Helm *et al*. 2009; Helm and Witkowski 2013). Marula trees are actively selected for by elephants and studies suggest that they are foraged more intensely than many other large tree species in South Africa (Weaver 1995; Trollope *et al*. 1998; Shannon *et al*. 2008; Henley 2013). Severe bark stripping has been recorded on various marula populations (Coetzee *et al*. 1979; Owen-Smith 1988; Helm *et al*. 2011a), with branch breaking as another common form of elephant impact (Gadd 2002; Jacobs and Biggs 2002a). Extreme herbivory such as stem snapping (also referred to as pollarding; O'Connor *et al.* 2007) and uprooting has also been recorded for trees taller than 2.5 m (Jachmann and Bell 1985; Jachmann and Croes 1991; Helm *et al*. 2009).

The decline in marula numbers is not, however, solely due to elephant impact. A lack of marula seedling recruitment is a concern in various marula populations (Helm *et al*. 2011a; Helm and Witkowski 2012). Seedling establishment can be affected by a variety of factors such as seed predation (Eriksson and Ehrlen 1992; Goheen *et al*. 2004), herbivory (Lewis 1987; Moe *et al*. 2009), climatic influence (Asner and Levick 2012), fire intensity (Trollope 1983; Jacobs and Biggs 2001), and trampling by megafauna (Lawes and Chapman 2006). Seed predation is a common seed fate that occurs once either primary or secondary seed dispersal has occurred (Helm *et al*. 2011a; Midgley *et al*. 2012). Parrots, rodents, as well as other small mammals have been recorded predating on marula seeds by manually opening the marula endocarps to feed on the stored seed (Palmer and Pitman 1972; Manson *et al*. 2001; Symes and Perrin 2003; Goheen *et al*. 2004). Marula seeds that develop into seedlings are highly palatable (Walker *et al*. 1986) and studies have indicated a negative correlation between marula seedling survival and herbivore densities, especially high densities of impala, (*Aepyceros melampus*) (Lewis 1987; Gadd 1997; Haig 1999; Kauffman and Maron 2006; Helm and Witkowski 2012). These environmental factors further compound the external pressures on marula populations, in conjunction with the elephant impact on adult individuals.

In January 2009, Helm and Witkowski (2012) assessed the size class distributions of marula populations across the Greater KNP. One of the study sites, Jejane Private Nature Reserve (JPNR), displayed a high-density adult dominated population with very little seedling recruitment. In addition, JPNR also had one of the highest levels of seed predation within the Greater KNP (Helm *et al*. 2011a). At the time of the 2009 assessments, JPNR had not had any elephants present within the reserve in over 100 years (G. Thomson, personal communication, November 23, 2016). In March 2013, JPNR proceeded to remove 15 km of fence-line bordering the Greater KNP, allowing for elephants to move into JPNR from bordering reserves (Thomson 2013). Therefore, by resurveying the marula trees within JPNR in 2016, this study assessed the changes in population dynamics of marula trees in JPNR since the migration of elephants in 2013 through the following objectives: (i) to assess elephant-induced impact and mortality levels on the previously surveyed JPNR marula population, (ii) to compare these levels to previously recorded impact and mortality levels on marula trees in central and southern KNP, and (iii) to assess marula seed predation and seedling recruitment to address its regeneration. I predicted that the number of marula trees in the larger height classes would be reduced because previous research has recorded that elephants actively feed off trees between the heights of 5 - 11 m (Shannon *et al*. 2008; Henley 2013). I predicted that the highest mortality rates and elephant impact scores would occur on trees between the heights of 5 - 11 m, as previous studies have recorded heavy elephant impact on marula trees between these heights (Jacobs and Biggs 2002a; Helm *et al*. 2009). I predicted that mortality rates in JPNR would be higher than those in KNP because of the high elephant densities combined with the creation of a novel feeding environment with numerous marula trees due to JPNR being fenced off from elephants for over 100 years and the increased water provision within JPNR (G. Thomson, personal communication, November 23, 2016). I also predicted that there would be high levels of seed predation and low levels of recruitment since the 2009 survey, because Helm and Witkowski (2012) previously recorded an adult-dominated marula population within JPNR with a lack of seedlings.

Materials and methods

Study area

JPNR is a 21 km² protected area situated in the southern region of Balule Nature Reserve (S24.29045; E30.97664). Balule Nature Reserve is one of four private nature reserves forming the Associated Private Nature Reserves (APNR), an area of 1,800 km² on the western border of the KNP, and is part of the Greater KNP (Figure 1). JPNR receives a mean annual rainfall of 400 - 600 mm (G. Thomson, personal communication, February 21, 2016) and is located in the Granite Lowveld vegetation unit (SVI 3) in the Savanna biome (Mucina and Rutherford 2006). This vegetation unit is a moderately open savanna that is dominated by tall tree species such as *Sclerocarya birrea*, *Combretum apiculatum* Sond. and *Senegalia nigrescens* Oliv. (Peel *et al*. 1993; Mucina and Rutherford 2006). The KNP is further to the east of JPNR along the South Africa-Mozambique border (Figure 1). Marula trees in the KNP were previously sampled in the marula-knobthorn savanna, Delagoa-thorn thickets, Sabie thorn thickets, Mixed bushwillow woodlands, and Gabbro thornveld ecozones (Grant and Thomas 2006; Helm *et al*. 2009). KNP receives a mean annual rainfall of 500 - 700 mm (Venter and Gertenbach 1986).

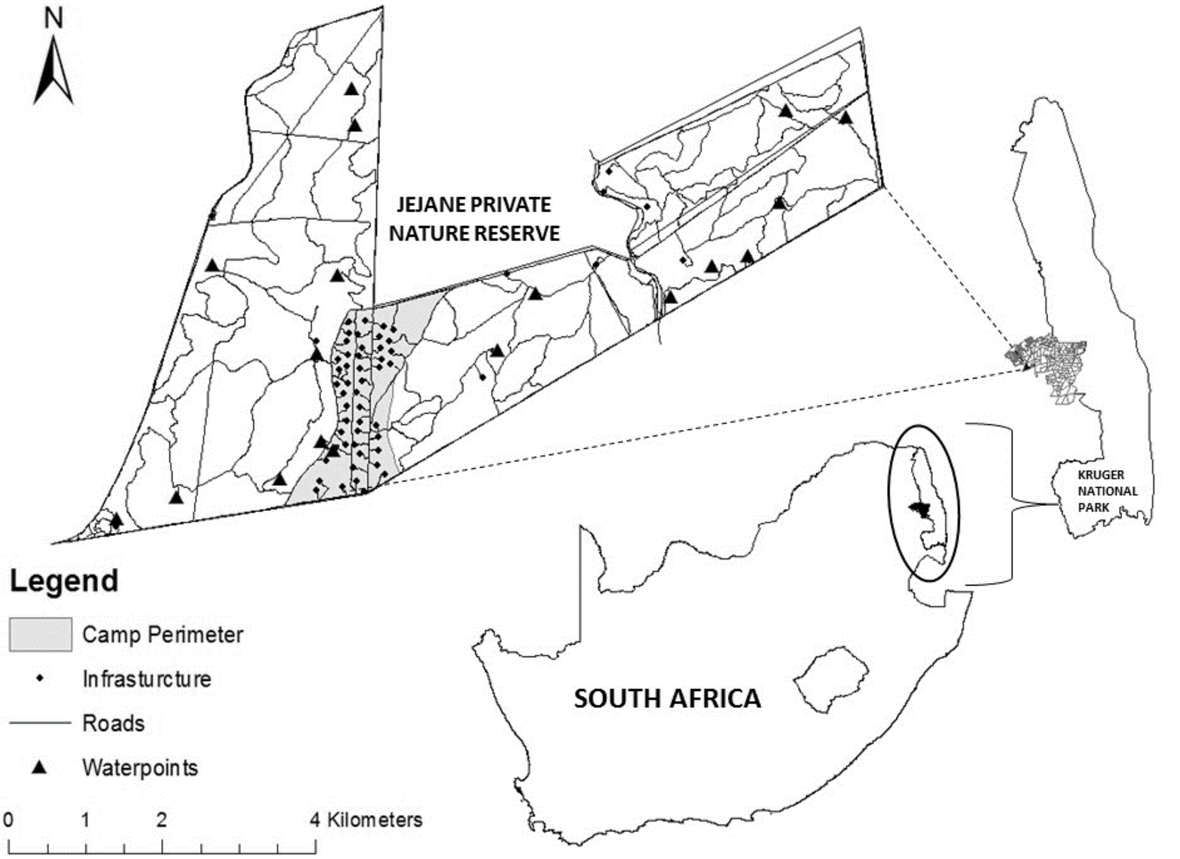

Figure 1: Location of Jejane Private Nature Reserve along the western border of the Associated Private Nature Reserves (APNR; western private reserves adjoining the Kruger National Park). The APNR forms a sectional region of the Greater Kruger National Park (Greater KNP).

Study species

The marula tree is a deciduous tree and keystone species, with both ecological and economic uses (Shackleton et al. 2002). Marula trees are dioecious, with the female trees producing fruit containing 0 - 4 seeds (Shackleton *et al*. 2002; Leakey *et al*. 2005). Marula trees are most prolific along well-drained soil crests with a mean annual rainfall of 200 - 1500 mm (Lewis 1987).

Elephant impact and mortality levels

From 29 April - 01 May 2016, 202 previously surveyed marula trees along 8 transects (Helm and Witkowski 2012) were resurveyed for elephant impact. These trees had not been assessed for elephant impact in the past. Transects were all 40 m in width and ranged from 203 - 289 m in length. All marula trees had been previously georeferenced using a Global Positioning System (GPS).

Upon arrival at the GPS location of each tree, the following methods were carried out, as previously described by Helm *et al*. (2009) and Helm and Witkowski (2012; 2013) - The located tree was classed into the following three tree fates: 'Surviving', 'Missing' and 'Dead'. Trees classified as 'Dead' were further categorised into the cause of the death, being 'Main stem snapped', 'Uprooting' or 'Bark stripping'. Trees that were classified as 'Surviving' had their height measured using the *VolCalc* digital photography method for estimating tree dimensions (Barrett and Brown 2012), with a level of accuracy of 1 cm. In order to compare height class distributions to those previously measured by Helm and Witkowski (2012), surviving trees were placed in the following 12 height classes: 1 ($\leq$ 0.25 m), 2 (0.25 - 1 m), 3 (1 - 2 m), 4 (2 - 3 m), 5 (3 - 4 m), 6 (4 - 5 m), 7 (5 - 6 m), 8 (6 - 8 m), 9 (8 - 10 m), 10 (10 - 12 m), 11 (12 - 15 m), and 12 (> 15 m). To compare Basal stem diameter (BSD) class distributions to those previously measured by Helm and Witkowski (2012), surviving trees were placed in the following 10 BSD size classes: 1 (0.5 - 2 cm), 2 (2 - 5 cm), 3 (5 - 9 cm), 4 (9 - 14 cm), 5 (14 - 20 cm), 6 (20 - 30 cm), 7 (30 - 40 cm), 8 (40 - 50 cm), 9 (50 - 60 cm), and 10 (60 - 70 cm). Adult marula trees were classified as trees with a BSD > 14 cm (Helm and Witkowski 2012). In order to compare elephant impact scores and mortality rates to KNP marula populations surveyed by Helm *et al*. (2009), the following 5 height classes were used: 1 (2 - 5 m), 2 (5 - 8 m), 3 (8 - 11 m), 4 (11 - 15 m), and 5 (> 15 m). BSD was measured 30 cm from the ground for each tree.

Surviving trees were further placed according to the following tree fate categories: 'Mature' (tree alive and > 2 m in height), 'Stem snapped' (main stem broken but tree coppicing), 'Toppled' (tree has been pushed over but coppicing), or 'Gulliver' (tree < 2 m in height and coppicing as a result of a previous fire). The following elephant impact scores, as previously used by Jacobs and Biggs (2002a), Helm *et al*. (2009) and Helm and Witkowski (2013), were used for 'Surviving' trees that were categorised as 'Standing' and 'Stem snapped'; 0: no damage; 1: < 50% of the bark around the main stem's circumference has been removed and/or secondary branches have been broken off; 2: > 50% of the bark around the main stem's circumference has been removed, or one primary branch has been broken off; 3: > 50% of the bark around the main stem's circumference has been removed and one primary branch has been broken off, or more than one primary branch has been broken off; 4: the tree has had its main stem snapped but is coppicing or alive. Additional notes were recorded on the presence of bracket fungus (class Basidiomycetes), termites (*Coptotermes* species), woodborer activity, or any other damaging insect activity (Vogel *et al.* 2014). The age of any elephant impact was estimated into the following age classes using parameters established by Henley (2013): 1 (recent, within the past month); 2 (1 - 6 months); 3 (6 - 12 months); and 4 (more than a year old). Marula trees are dioecious (Shackleton *et al*. 2002), and previous research has indicated that elephants may have a preference for female trees because of the fruit they bear (Hemborg and Bond 2007). Therefore the sex of each tree was determined by searching for fruit endocarps below the tree's canopy (Helm *et al*. 2009; Helm *et al*. 2011a).

Proportions were used to represent the number of trees in each of the tree fate and impact score classes, as well as the height and BSD size class distributions. Shapiro-Wilks normality tests were applied to test for normality. A Kolmogorov-Smirnov two-sample test was used to test for differences in the height and BSD size class distributions between 2009 and 2016. A Kruskal-Wallis by ANOVA Rank test, with Dunn's multiple comparison post-hoc test, was used to test for impact score differences between height classes in JPNR. Furthermore, tree height selection by elephants was assessed using preference ratings (Petrides 1975) to identify if elephants were targeting a specific height class. Marula tree densities were calculated as the number of individuals per transect area (marula trees/ha). A paired t-test was used to test for differences between the marula densities of 2009 and 2016, whilst a Chi-squared test was used to test for differences in the JPNR marula sex ratio between 2009 and 2016. Tree fates, elephant impact scores and tree annual mortality rates (AMR) in JPNR were compared to those in central and southern KNP surveyed by Helm *et al*. (2009). A Mann-Whitney U-test was used to test for impact score differences between JPNR trees in 2016 and KNP trees in 2001 and 2008, respectively. Annual mortality rates were divided into two separate time periods for JPNR, 2009 - 2016 and 2013 - 2016. The 2009 - 2016 AMR assumed that marula tree mortality occurred both prior- and post- elephant migration of elephants due to fence removal, whilst the 2013 - 2016 AMR assumed that marula tree mortality occurred predominantly post-elephant migration in 2013. All statistical analyses were performed using R statistical software (R v. 3.2.2) with a significance level of 0.05 (R Core Team 2016).

Seed predation and seedling recruitment

Seed bank sampling methods were carried out from 02 - 03 May 2016 following methods by Helm *et al*. (2011a). Ten female marula trees from each of the following BSD size classes (< 30 cm; 30 - 40 cm; and > 40 cm) were sampled. The presence of endocarps beneath the tree's canopy was used to indicate a female tree (Helm *et al*. 2009; Helm *et al*. 2011a). For each tree, the following microsites were assessed: inner canopy (trunk to half radius of tree canopy); outer canopy (half radius of tree canopy to canopy edge); subcanopy (trunk to canopy edge); and outside canopy (< 10 m outside of canopy edge). A total of eight quadrats (0.5 x 0.5 m) were sampled for each tree. Four quadrats were sampled in the inner canopy of each tree on the northern, southern, western and eastern bearings of the trunk. Two quadrats were sampled within the outer canopy of each tree on the northern and southern bearings of the tree trunk, and two quadrats were randomly sampled outside the canopy of each tree, > 5 m apart from one another other. For each quadrat, marula endocarps within the litter layer and the soil layer (5 cm in depth) were collected. Endocarps were separated from the soil and debris using a 120 x 70 cm sieve (12 mm diameter holes). Each endocarp was labelled according to its microsite, quadrat bearing, layer position, as well as the tree's BSD category. Further notes were taken on whether each endocarp had flesh, dried skin or pulp surrounding it, indicating that the endocarp was 'new' and from the most recent fruiting season. For each marula endocarp collected, the total number of locules were recorded, representing the total number of potential seeds per endocarp prior to primary dispersal. Of these locules, the total number of open and closed locules were recorded. The number of open locules (operculum removed) was indicative of the number of seeds that had been removed from the endocarp, representing either seed predation or germination. The number of closed locules (intact operculum) was indicative of the number of potential seeds still present within the endocarp. The presence of bite marks on the operculum were also recorded.

The presence and number of marula seedlings and saplings were recorded in each of the eight transects. Each transect had a search effort of one hour, with each female tree having an additional search effort of ten minutes. Seedlings were placed into one of the following seedling height classes: 1 ($\leq$ 0.25 m) and 2 (> 0.25 - 1 m). Seedlings in height class 1 represented new seedlings from the current season, whilst seedlings in height class 2 represented older seedlings from previous years.

A Kruskal-Wallis by ANOVA Rank test, with Dunn's multiple comparison post-hoc test, was used to compare endocarp densities between microsites, and a Wilcoxon signed-rank test was used to test for differences in endocarp densities between the litter and soil layers across the microsites.

Results

Elephant impact and mortality levels

Of the 202 resurveyed trees in JPNR, there was an increase in the number of marula trees within the lower height classes (classes 1 - 7) as a result of the main stem snapping of trees in larger height classes from the 2009 survey. The distribution of live individuals in the twelve height classes in 2009 differed significantly to the height class distribution of live individuals in 2016 ($D = 0.56$; $p <$

0.00001) (Figure 2a). There was a general increase in BSD size across the sampled population but the distribution of live individuals in the ten BSD classes in 2009 did not differ significantly to that in 2016 ($D = 0.11$; $p = 0.29$) (Figure 2b). Overall, JPNR still displayed an adult dominated population with most trees in the larger height and BSD size classes.

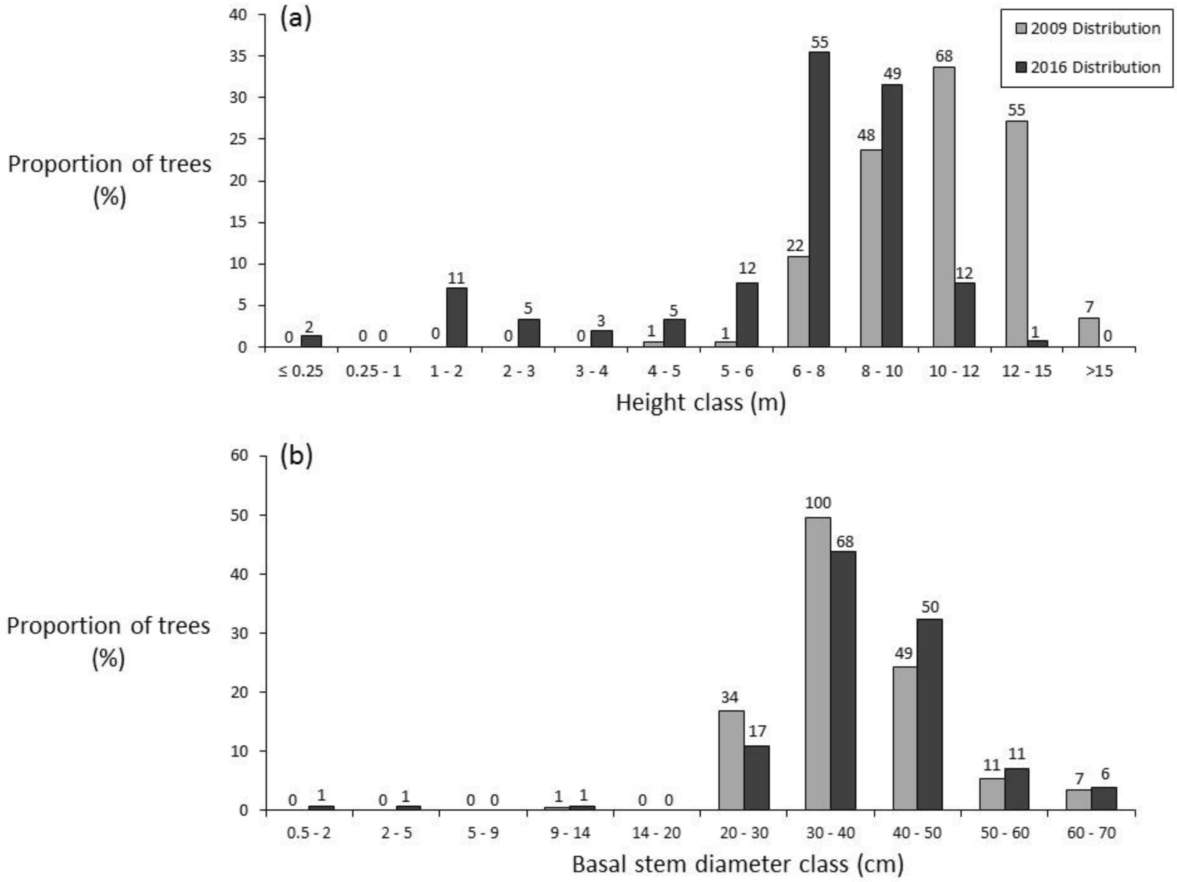

Figure 2: Changes in **(a)** height and **(b)** basal stem diameter class distributions of marula trees in Jejane Private Nature Reserve between 2009 (Helm and Witkowski 2012) and 2016 assessments. Numbers above each bar represents the number of live trees in each height and basal stem diameter class. There were significant decreases in marula tree heights since the migration of elephants due to fence removal, whilst no significant differences were recorded in basal stem diameter class distributions between 2009 and 2016.

Of the resurveyed trees in JPNR, 23.8% ($n = 48$) were dead, whilst the highest proportion of trees were categorised as alive and mature (64.3%, $n = 130$) (Figure 3). In the KNP marula population that was resurveyed in 2008, 13.7% ($n = 65$) of the trees were dead, with 43.7% of the trees alive and mature ($n = 207$, Figure 3). Although differences in the proportions of dead versus live trees were similar across most tree fates between the JPNR and KNP marula populations, notable differences were observed in the ‘Missing’ and ‘Gulliver’ categories. A total of 16.7% of marula trees in KNP were missing from 2001 to 2008, whilst only 1 tree in JPNR (previously 9.8 m in height) could not be located (Figure 3). KNP also had 17.1% (*n* = 81) of the resurveyed trees in a Gulliver state, whilst this tree fate was not found in JPNR. It was also noted that 100% (*n* = 201) of the resurveyed and located trees in JPNR had woodborer activity, whilst 66.7% (*n* = 134) had termite activity, and 3% (*n* = 6) had fungi present.

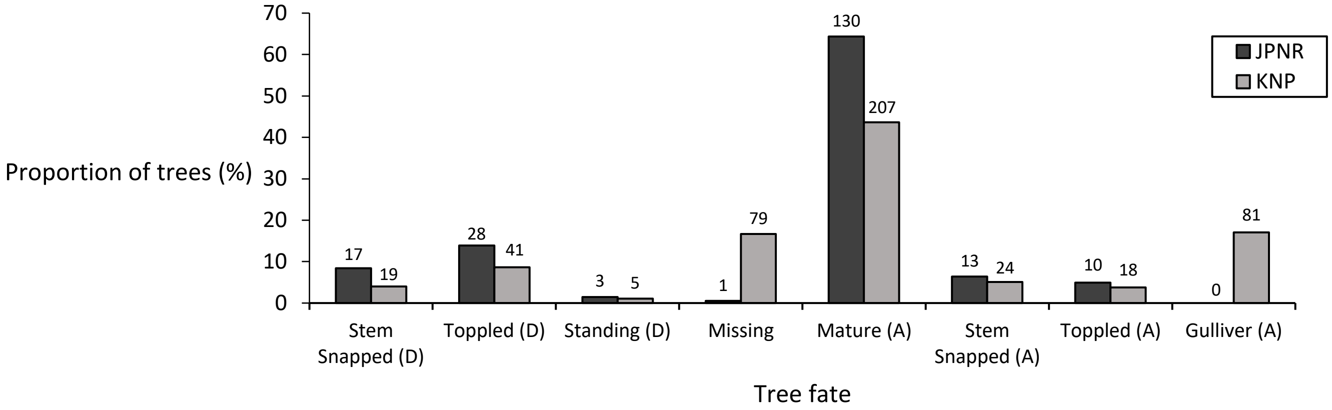

Figure 3: Comparison of the tree fate of resurveyed marula trees between Jejane Private Nature Reserve (*n* = 202) and the central and southern regions of the Kruger National Park (*n* = 474) (Helm *et al*. 2009). Numbers above each bar represents the number of trees in each tree fate. 'A' represents trees which are alive; 'D' represents trees which are dead.

Of the resurveyed marula trees in JPNR, 82% of the elephant impact was > 1 year old (age class 4), placing this impact within the first 2 years that JPNR has had elephants, whilst 6.5% of the total impact had occurred within one month prior to surveying (age class 1). Impact scores on the resurveyed trees differed significantly across the height classes ($H_{(3)} = 9.579$; $p < 0.05$ 0.03; $n = 153$), with a mean rank score of 97.6 for 5 - 8 m, 83 for 8 - 11 m, 66 for 11 - 15 m, and 76.1 for > 15 m (Figure 4). There was no significant difference between male and female marula trees' impact scores ($U = 4641$; $p = 0.33$; $n_{♀} = 89$; $n_{♂} = 112$), nor was there a significant change in the JPNR male-to-female sex ratio between 2009 (1 male: 1.26 females) and 2016 (1 male: 1.39 females) ($\chi^2_1 = 0.184$; $p = 0.89$; $n_{2009} = 202$; $n_{2016} = 153$), with 24 female and 25 male marula trees found dead.

Elephant impact scores on marula trees from JPNR in 2016 were higher than impact scores recorded on KNP trees in 2001, and equal to or lower than impact scores recorded on KNP trees in 2008 (Figure 4). In height class 2 (5 - 8 m), JPNR elephant impact scores were significantly higher than those in KNP_{2001} ($U = 69.5$; $p < 0.05$; $n_{JPNR} = 15$; $n_{KNP} = 18$), whilst there was no significant difference in the comparison to KNP_{2008} impact scores ($U = 71.5$; $p = 0.14$; $n_{JPNR} = 15$; $n_{KNP} = 14$). Similar results were recorded in height class 3 (8 - 11 m), where elephant impact scores in JPNR were significantly higher than those in KNP_{2001} ($U = 842.5$; $p < 0.00001$; $n_{JPNR} = 62$; $n_{KNP} = 58$), whilst there was no significant difference in the comparison to the KNP_{2008} impact scores ($U = 1126.5$; $p = 0.42$; $n_{JPNR} = 62$; $n_{KNP} = 40$). JPNR elephant impact scores in height class 4 (11 - 15 m) were significantly higher than those in KNP_{2001} ($U = 3471$; $p < 0.001$; $n_{JPNR} = 68$; $n_{KNP} = 140$), but were significantly lower than the impact scores in KNP_{2008} ($U = 2741.5$; $p < 0.00001$; $n_{JPNR} = 68$; $n_{KNP} = 131$). Height class 5 (> 15 m) impact scores were significantly higher in JPNR compared to KNP_{2001} ($U = 17$; $p < 0.01$; $n_{JPNR} = 7$; $n_{KNP} = 15$), whilst there was no significant difference between the impact scores of JPNR and KNP_{2008} ($U = 86.5$; $p = 0.83$; $n_{JPNR} = 7$; $n_{KNP} = 26$).

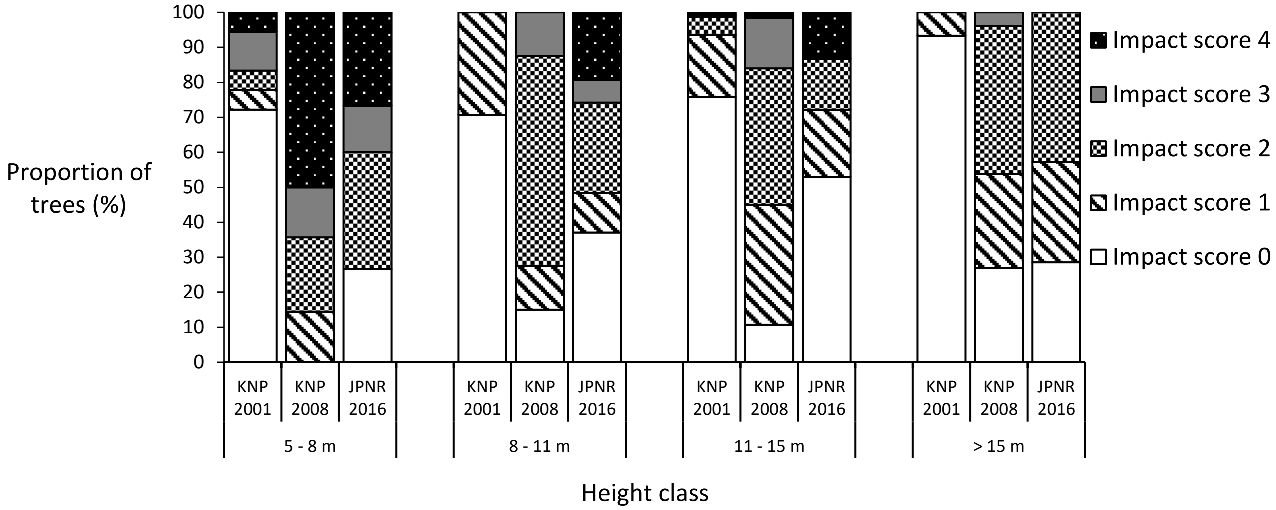

Figure 4: Comparison of elephant impact score across marula tree height classes between Jejane Private Nature Reserve (2016) and the Kruger National Park (2001 and 2008; *Helm et al.* 2009). Highest elephant impact levels were recorded in the 5 - 8 m and 8 - 11 m height classes.

There was a significant decrease in the JPNR marula density from 25.6 ± 2.3 trees/ha in 2009 to 19.6 ± 2.2 in 2016 ($t_{(7)} = 7.61$; $p < 0.001$; $n = 8$). The highest total mortality (2009 - 2016) in JPNR occurred in the 5 - 8 m height class (35.3%), followed by the 8 - 11 m height class (28.2%) (Figure 5a). Elephants displayed a high preference rating for trees in the 5 - 8 m height class (Table 1). Similarly, in central and southern KNP, the highest mortalities were also recorded in the 5 - 8 m height class (58.3%; Helm *et al*. 2009), followed by the 8 - 11 m height class (28.2%, Helm *et al*. 2009) (Figure 5a). For calculations done for 2009 - 2016, the AMR of trees in JPNR (3.5% per annum) was lower than the AMR of trees in KNP (4.6% per annum). However, for calculations done for 2013 - 2016, the JPNR AMR of 8.1% per annum was higher than that of KNP. The highest AMRs occurred in the smaller height classes for both JPNR and KNP (Figure 5b). For calculations done for 2009 - 2016, JPNR AMRs were equal to or smaller than AMRs in KNP across most height classes (Figure 5b). For calculations done for 2013 - 2016 however, AMRs of marula trees in JPNR were always greater to those of KNP.

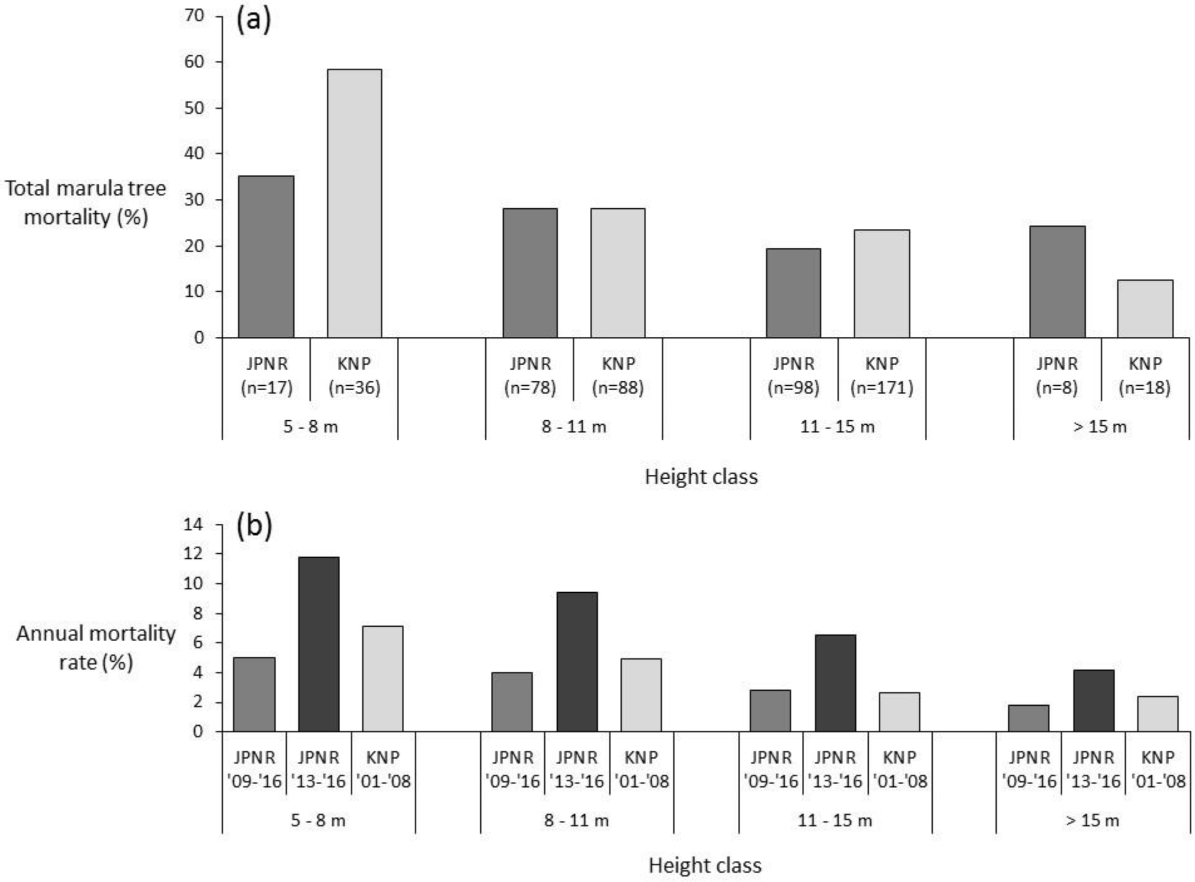

Figure 5: Marula tree **(a)** total mortality percentage and **(b)** annual mortality rates across marula tree height classes in Jejane Private Nature Reserve (*n* = 201) and the Kruger National Park (*n* = 313, Helm *et al*. 2009). Annual mortality rates for JPNR were divided into two time periods: '2009 - 2016', assuming tree mortality had occurred prior to the migration of elephants in 2013; and '2013 - 2016', assuming tree mortality only occurred post- elephant migration in 2013.

Table 1: Elephant preference ratings for marula tree height classes in Jejane Private Nature Reserve (using original heights from Helm and Witkowski (2012)). Preference ratings > 1.00 indicate that the height class is sought after or preferred by elephants.

Height class	**Quantities**		**Preference rating**
	Trees available	**Trees removed**	
5 - 8 m	17	7	1.69
8 - 11 m	78	22	1.16
11 - 15 m	98	19	0.80
> 15 m	8	1	0.51
Totals	201	49	-

Seed predation and seedling recruitment

A total of 1,033 endocarps were collected and analysed from 30 female marula trees. The number of locules present per endocarp ranged from 1 - 4 (mean ± S.E. = 2.2 ± 0.02). Endocarp density differed significantly across the microsites ($H_{(3)} = 65.253$; $p < 0.0001$; $n = 1,033$), with a mean rank score of 85.4 for the inner canopy, 56.6 for the outer canopy, 80 for the subcanopy, and 20.3 for the outside canopy (Figure 6). Most endocarps (81.6%; $n = 843$) were found in the litter layer compared to the soil layer (18.4%; $n = 190$) for all microsites (Figure 6).

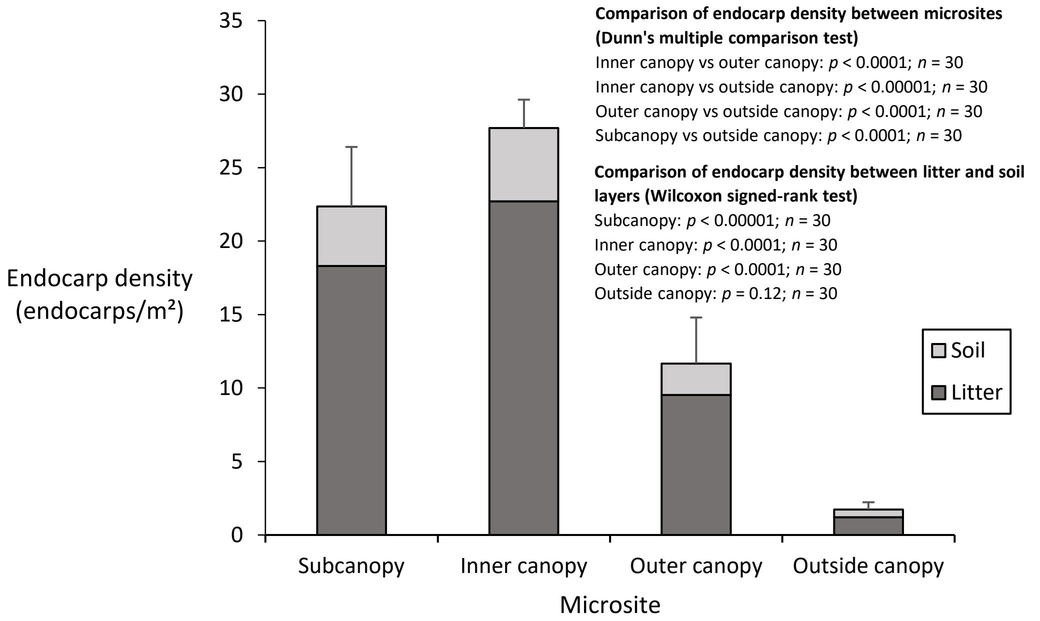

Figure 6: Endocarp density (endocarps/m²; mean ± SE) between the litter and soil (0 - 5 cm depth) layers across the four microsites of 30 female marula trees in Jejane Private Nature Reserve. The highest endocarp densities were found in the litter layer of the inner canopies.

Of the sampled endocarps, 97.1% ($n = 1,003$) had at least one missing seed, and 42.3% ($n = 307$) had bite marks along at least one of the opercula. Only 2.1% ($n = 22$) of the endocarps were untouched and had all of the locules enclosed with no bite marks present. A total of 2,289 locules were counted from the 1,033 endocarps, of which 84.2% ($n = 1,928$) had been opened and had empty locules. Four endocarps still had a fleshy covering, indicating that they were from the most recent fruiting season. Of the fleshy endocarps, 6 of the 7 opercula had been removed and the locules were empty, indicating a seed predation level of 85.7% on these new seeds.

A total of only two seedlings were recorded (both in seedling height class 1) across all transects. Both seedlings were located under the subcanopy of female trees within 4 m of the main stems. Both seedlings were situated south of their parent tree.

Discussion

Elephant impact and mortality levels

There was a significant shift in the number of JPNR marula trees from higher to lower height classes, with the highest elephant impact scores occurring in height classes 2 (5 - 8 m) and 3 (8 - 11 m). The resurveyed marula population had declined by 23.8% over a three year period since the migration of elephants due to fence removal, with the highest AMRs in height classes 2 (11.8%) and 3 (9.4%). AMRs in JPNR were higher than those in KNP.

The significant shift in the number of JPNR marula trees from higher to lower height classes was largely due to main stem breakage and primary branch breakage. Stem and branch breakage alters a tree's growth and can lead to coppicing (Coetzee *et al*. 1979; Lewis 1991). Coppicing and stunted or hedged growth forms were identified on a number of trees that were alive but had been modified by elephants. Although there was no significant change in the number of trees across the BSD size classes, diameter at breast height (DBH) measurements may have revealed a more accurate pattern of elephant impact because of the cross-sectional areas of coppiced shoots in comparison to intact basal stems. In KNP, there were many more marula trees classified by Helm *et al*. (2009) as 'Missing' and 'Gulliver' in comparison to JPNR. The GPS locations of the KNP marula trees were originally recorded in 2001 but not physically marked (M. Hofmeyr, unpublished data). Therefore, some trees were either not located as a result of possible GPS error, or the smaller trees may have completely burnt away from previous fires (Shannon *et al*. 2008; Helm *et al*. 2009). There is a no-fire policy in JPNR, which would have also resulted in the differences in number of 'Gulliver' trees (tree < 2 m in height and coppicing after fire) in KNP in comparison to JPNR. JPNR trees were not at risk to fire-damage between the two sampling periods, however, a high number of individuals had either termite- or wood borer- activity (personal observation). Termites in trees is particularly prevalent in unburnt savannas (Abensperg-Traun and Milewski 1995) and could result in the deterioration of individuals from the inside (Cowie *et al*. 1989). This deterioration causes these trees to become hollow, and therefore more vulnerable to being toppled over by wind and elephants (Hofmeyr 2003), as well as being more vulnerable to fire (Helm *et al*. 2011b).

In KNP, Jacobs and Biggs (2002a) measured heavy elephant impact on marula trees between 5 - 11 m in height, whilst Shannon *et al*. (2008) found the greatest proportion of toppled marula trees in the 5 - 8 m height class. The preferred feeding height of elephants is 2 - 3 m (Jachmann and Croes 1991), and so elephants may push over taller trees to gain access to out of reach portions of these trees (Jachmann and Bell 1985; Stokke and Du Doit 2000). The high preference ratings for marula trees 5 - 8 m in height further supports the suggestion that elephants are actively seeking out trees that they can physically modify in order to browse (Croze 1974; Petrides 1975). Elephant bulls are more likely to explore newly opened regions in comparison to breeding herds (Druce *et al*. 2008), and an early study indicated a high presence of young 'pilot' bulls in JPNR post-fence removal (Weber 2014). Bulls are hypothesised to heavily impact trees as an act of 'confidence building' and muscular training, in addition to browsing activities (Croze 1974; Guy 1976; Midgley *et al*. 2005). It is likely that the high levels of elephant impact on JPNR's marula trees was a direct result of an initial influx of elephants, particularly bulls, into the reserve. During the first year that the fence was removed (2013), the elephant density in JPNR and the immediate surrounding reserves (estimated using an aerial census) was 2.16 elephants/km^2, dropping to 0.69 elephants/km^2 in 2014 and rising to 1.5 elephants/km^2 in 2015 (G. Thomson, personal communication, September 06, 2016). The initial JPNR elephant density in 2013 was more than double that of the current KNP elephant density (0.88 elephants/km^2; Chase *et al*. 2016), and these high elephant densities may explain why almost a quarter of the resurveyed marula trees in JPNR had died after three years since the fence-line was taken down. Future studies will be required to investigate how the loss of adult trees within these height classes will affect the distribution of species which may be reliant on them, including vultures, which may use these trees as nesting sites (Vogel *et al*. 2014), or Southern Ground-hornbill (*Bucorvus leadbeateri*) (Wilson and Hockey 2013).

Although tree mortality can occur from the effects of wind (Jacobs and Biggs 2002a) and insects (Haig 1999; Gadd 2002), it is unlikely that marula tree mortality between 2009 and 2012 is of the same scale as between 2013 and 2016 (once elephants had migrated into JPNR). Furthermore, the fuel loads within JPNR are generally too low to carry a fire, and no wild fires occurred within the 2009 - 2012 period (G. Thomson, personal communication, January 10, 2017), which could have killed smaller marula trees and seedlings (Jacobs and Biggs 2001; Shannon *et al*. 2008; Helm *et al*. 2011b). Therefore, the 2013 - 2016 AMR calculations are a more accurate estimate of JPNR marula tree mortality between sampling periods. During the Helm *et al*. (2009) study period, the elephant density in KNP increased from 0.41 elephants/km^2 in 2001 to 0.66 elephants/km^2 in 2008 (Scientific Services, SANParks). These elephant densities were lower than those of JPNR between 2013 and

2015 and may explain why the mortality rates of marula trees in JPNR were greater than those recorded in the KNP study by Helm *et al*. (2009). Furthermore, JPNR had not had any elephants present in the region in over 100 years and had the highest density of adult marula trees (BSD > 14 cm) in the Greater KNP prior to elephant migration due to fence removal (Helm and Witkowski 2012). Although marula tree density significantly decreased from 25.6 trees/ha to 19.6 trees/ha, JPNR would still have the highest adult marula density in the Greater KNP according to the Helm and Witkowski (2012) results. The high marula tree density, coupled with the high elephant density, increases the probability of encounter between elephants and marula trees, thereby increasing marula mortality levels (O'Connor *et al*. 2007). In subsequent years, the high marula AMRs in JPNR may decrease as the abundance of marula trees decreases. Helm and Witkowski (2013) recorded a decrease in marula tree AMRs between the sampling years of 2008 - 2009 (4.6%) and 2009 - 2010 (3.2%). Future studies will be required to determine if and when the JPNR AMR of 8.1% per annum decreases to AMRs observed in KNP. However, the increased number of JPNR trees in smaller height classes as a result of main stem snapping by elephants may further influence the AMRs, as these individuals may become more vulnerable to increased levels of herbivory by browsers, as well as any wild fires which may arise within the system (Jacobs and Biggs 2001; Helm *et al*. 2011b).

Seed predation and seedling recruitment

Of the sampled endocarps, 97.1% had at least one seed missing, whilst 84.2% of the endocarp locules had been opened. Furthermore, 69.4% of the sampled endocarps were in the litter layer. Only 2 marula seedlings ($\leq$ 25 cm in height) were found across transects, indicating a lack of recruitment in the JPNR marula population.

Seeds that fall onto the soil surface are subject to seed predation from birds, insects, and rodents (Hulme 1998; Kolb *et al*. 2007; Bricker and Maron 2012). Some seeds are able to escape predation through abiotic burial into the soil layer (Chambers *et al*. 1991; Garner and Witkowski 1997). However, abiotic burial is reliant on both the seed and soil characteristics (Chambers *et al*. 1991; Thompson *et al*. 2000). Seeds with large endocarps, such as marula seeds, do not easily enter the soil layer (Thompson *et al*. 1993), leaving these seeds exposed in the litter layer and vulnerable to seed predators (Reader 1991). Helm *et al*. (2011a) recorded marula seed predation levels of 19 - 30% within the KNP (Helm *et al*. 2011a). However, the seed predation level of new marula endocarps in JPNR between January and May 2009 was 70% (Helm *et al*. 2011a), and 6 of the 7 locules (85.7%) of the 4 new (fleshy) endocarps in this study had been predated. These results suggest that marula recruitment in JPNR may also be seed limited. Tree squirrels (*Paraxerus cepapi*) function as both marula seed dispersal agents and predators, manually removing the operculum to feed on the seed within the locule (Midgley *et al*. 2012). A lack of fire in savannas can result in an increase in vegetation cover (Trollope 1982; Stephens *et al*. 2009), thereby leading to an increase in rodent numbers and seed predation (Reader 1991; Briani *et al*. 2004; Helm *et al*. 2011a). High levels of seed predation could ultimately cause seed limitation within a population, restricting the recruitment and regeneration of its individuals into both seedling and adult demographic stages (Kurkjian *et al*. 2016).

JPNR displayed an adult-dominated marula population (Group 1 classification; Helm and Witkowski 2012), evident by the lack of individuals with a BSD < 14 cm. Marula with a group 1 population structure are representative of a population where recruitment has not occurred in many years, representing a pattern of distinct episodic recruitment (Helm and Witkowski 2012). Similar episodic recruitment patterns have been identified for *Adansonia digitata* L. in South Africa (Venter and Witkowski 2010) and *Vachellia tortilis* subsp. *raddiana* Forssk. in Israel (Wiegand *et al*. 2000). Populations that experience such bottlenecks at the seed and seedling levels are potentially proceeding towards local extirpation (O'Connor *et al*. 2007). In 2009, Helm and Witkowski (2012) did not find any seedlings in JPNR, indicating a lack of recruitment in this population prior to elephant migration into JPNR. A number of factors affect seedling recruitment, including seed limitation (Eriksson and Ehrlen 1992), herbivory (Moe *et al*. 2009), fires (Jacobs and Biggs 2001) and rainfall (Venter and Witkowski 2013). Impala are one of the main seedling predators in African savannas and various studies have found correlations between increased impala densities and a decrease in seedlings (Lewis 1987; Mosugelo *et al*. 2002; Skarpe *et al*. 2004; Moe *et al*. 2009). The mean impala density in JPNR and the immediate surrounding reserves was 17.74 ± 5.29 individuals/km^2 between the years 2010 and 2015 (G. Thomson, personal communication, September 06, 2016). This is higher than the neighbouring KNP impala density, ranging from 8.12 - 11.7 individuals/km^2 across the reserve (Ferreira *et al*. 2013). Thus, the high impala densities, combined with trampling by larger herbivores around adult trees (Lawes and Chapman 2006), may be preventing marula seedlings from developing into saplings and adults.

Successful recruitment of long-lived savanna trees is also reliant on favourable conditions, including long periods of soil moisture and low seed and seedling predation levels (Wilson and Witkowski 1998). Although not directly tested in this study, stable marula populations have been shown to be associated with high rainfall sites, even in the presence of elephants (Helm and Witkowski 2012). Water stress can have negative effects on the recruitment success of long-lived tree species (Otieno *et al*. 2001; Wiegand *et al*. 2004; Venter and Witkowski 2013) and JPNR had experienced two consecutive dry years prior to this study (< 270 mm per year; G. Thomson, personal communication, February 21, 2016). However, the lack of seedlings found in JPNR in 2009 by Helm and Witkowski (2012), after a relatively high rainfall year (605 mm; G. Thomson, personal communication, February 21, 2016), suggests that high levels of seed and seedling predation may be the main factors limiting the regeneration of marula trees in JPNR, even during periods of high rainfall.

Conclusion and management implications

Since the migration of elephants into JPNR, there has been a 23.8% decline in sampled marula trees, of which the highest mortality rates have occurred in trees 5 - 11 m in height. Although JPNR still has a high density of adult marula trees as a result of having no elephants in the reserve for over 100 years, there appears to be a lack of recruitment as a result of high levels of seed predation and the potential over-browsing of seedlings. The JPNR marula population may be facing local extirpation as a result of the high AMRs of adult trees and a lack of recruitment, with high seed predation levels and elephant impact as possible drivers. Elephant culling in the Greater KNP has been discontinued due to a combination of animal welfare concerns and evidence that elephant culling did not meet conservation goals (Owen-Smith *et al*. 2006). There has also been a scientific paradigm shift towards managing the impacts and distributions of species, rather than species' numbers alone (Owen-Smith *et al*. 2006; Ferreira *et al*. 2011; Ferreira *et al*. 2012; DEA 2013). Impala and elephant distributions, specifically, are positively correlated with the presence of rivers and artificial waterholes (Smit *et al*. 2007a and b). JPNR and the immediate surrounding reserves currently have an artificial waterhole density of 1 per 1.78 km² in the wet, and 1 per 3.35 km² in the dry season (G. Thomson, personal communication, December 06, 2016). These artificial waterhole densities are far greater in comparison to KNP (1 per 88.57 km², depending on the waterhole closure plan; Gaylard *et al*. 2003). Therefore, by decreasing the availability of surface water in JPNR, a change in the distribution of these two species may occur, decreasing the impact on adult marula trees and seedlings (Redfern *et al*. 2003; Chamaillé-Jammes *et al*. 2007). Mitigation methods have also been developed to directly influence elephant impact on large trees. These include sharp rocks stacked around a tree's main stem (SANParks 2012), wire-netting a tree's main stem to prevent bark-stripping (Henley 2013; Derham *et al*. 2016), and most recently, the use of African honeybees to deter elephants from impacting trees (refer to next chapter). Non-lethal elephant mitigation methods such as these, along with a carefully formulated artificial waterhole management plan (Purdon and Van Aarde 2017), could help reduce browsing pressure on both adult marula trees and seedlings, thereby allowing for possible marula regeneration from non-predated seeds. Furthermore, the use of enclosures which prevent herbivory could help adult marula trees establish within the system (Jacobs and Biggs 2002b).

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Chapter 3

African honeybees as a mitigation method for elephant impact on marula trees in the Greater Kruger National Park

Abstract

There are concerns in South Africa over the effects of the potentially high African elephant (*Loxodonta africana*) population density on the abundance and diversity of large tree species. In Kenya, research has shown that elephants actively avoid contact with swarms of African honeybees (*Apis mellifera* subsp. *scutellata*), avoiding crop fields surrounded by beehive fence-lines and moving away from the playback recordings of swarming honeybees. Therefore this study's objectives were (i) to test whether the presence of beehives in marula trees influenced the likelihood of the tree receiving elephant impact and compare these results to wire-netted trees (a method experimentally used to prevent ring-barking by elephants); (ii) to assess if elephants avoided areas with marula trees containing beehives; and (iii) to provide a comparison of the financial costs associated with the beehive and wire-netting mitigation methods. Fifty active beehives were hung from 50 marula trees, with 50 dummy (inactive) beehives hung on branches on the opposite ends of each tree's main stem. Another 50 marula trees were wire-netted and a further 50 marula trees were used as control trees. Elephant impact on all 150 trees was measured prior to the addition of treatments and then post-treatment addition for nine months. Elephant dung transects were carried out in the beehive site and a control site to investigate whether the presence of beehives affected elephant locations. Of the control trees, 54% 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 marula trees against bark-stripping but did not prevent elephants from breaking primary and secondary branches. Beehives, both active and inactive, proved efficient at preventing elephants from impacting marula trees in any form, although the presence of beehives in marula trees did not prevent elephants from moving through the beehive site. The financial cost and maintenance required for the beehive mitigation method is significantly higher than that of wire-netting, but the beehives can provide honey and pollination services as an additive benefit.

Keywords: *Apis mellifera* subsp. *scutellata*, Jejane, Kruger National Park, *Loxodonta africana*, mitigation methods, *Sclerocarya birrea* subsp. *caffra*, wire-netting

Introduction

Human-elephant conflict (HEC) occurs in a variety of scenarios where humans and elephants (*Loxodonta africana* Blumenbach 1797) share or compete for the same resources (O'Connell-Rodwell *et al*. 2000; Sitati *et al*. 2003; Cook *et al*. 2015). Although HEC primarily takes place along the agricultural interface (Sukumar 1991; Hoare 1999; Sitati *et al*. 2005; King *et al*. 2011), in South Africa, HEC is predominantly centred around elephant impact on large tree species in fenced-off protected areas (Cumming *et al*. 1997; Whyte *et al*. 2003; Helm and Witkowski 2013). Conservation strategies of enclosing elephant populations into protected areas have brought about a steady increase in South Africa's elephant numbers from the verge of local extinction (Carruthers 1995), to the 6th highest elephant population density in Africa (Chase *et al*. 2016). South Africa's growth in elephant numbers is a conservation success story in comparison to the decline of many elephant populations across Africa (Whyte 2001; Wittemyer *et al*. 2014; Chase *et al*. 2016). However, the increased elephant densities in South Africa have raised concerns over the impact that elephants have on large tree species and the potential ecological (Trollope *et al*. 1998; Shannon *et al*. 2008; Asner *et al*. 2015) and aesthetical (Edge *et al*. 2017) effects of the impact. Elephants display selective preferences amongst large tree species (Ihwagi *et al*. 2012), with marula (*Sclerocarya birrea* (A. Richard) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae)) in particular, being one of the preferred forage choices (Weaver 1995; Greyling 2004, Shannon *et al*. 2008; Henley 2013). Elephant impact on marula trees has been researched in South Africa as a result of the tree's cultural, economic, and ecological importance (Shackleton *et al*. 2002; Helm and Witkowski 2012; 2013). In South Africa's Greater Kruger National Park (Greater KNP), marula trees have been severely bark-stripped, toppled, or had their main stems snapped by elephants (Coetzee *et al*. 1979; Gadd 2002; Jacobs and Biggs 2002; Helm and Witkowski 2013), with trees under 8 m in height being particularly vulnerable to severe elephant impact (Jacobs and Biggs 2001; Helm *et al*. 2009). A study on the marula population in Jejane Private Nature Reserve (JPNR), a reserve within Greater KNP and the study site of this chapter, found that the resurveyed marula population has declined by 23.8% (8.1% per annum) since the migration of elephants in 2013. Elephants have not been present within JPNR for over 100 years and landowners and management have now expressed concern over the impact that elephants are having on the marula population (Weber 2014).

The current South African Elephant Research Strategy (2012 - 2023) focuses on altering elephants' spatial and temporal access to resources, thereby managing elephant effects rather than elephant numbers (Ferreira *et al*. 2012; SANParks 2012; DEA 2013). This policy of adaptive management allows for the trial and usage of novel techniques to mitigate elephant impact on large trees. A variety of elephant mitigation methods have been developed, including chilli extracts (Parker and Osborn 2006), stone walls (Omondi *et al*. 2004), trenches (MacKenzie 2012), flares, and fireworks (Hoare 2001). One such method that has been used to mitigate elephant impact on large trees is wire-netting (Gordon 2003; Henley 2013; Derham *et al*. 2016). Wire-netting, a cost-effective method which makes it applicable for large-scale usage, involves wrapping chicken-mesh around the main stem of a tree in an attempt to prevent severe bark-stripping. Wire-netting has prolonged the survival rate of large trees in the Timbavati and Klaserie Private Nature Reserves (Henley 2013; Derham *et al*. 2016). However, wire-netted trees are still vulnerable to branch breakage, main stem snapping and uprooting by elephants (Henley 2013; Derham *et al*. 2016). Branch breakage in particular may not directly kill the individual tree, but will render it vulnerable to the invasion of woodborers, which may ultimately kill the tree (Coetzee *et al*. 1979; Jacobs and Biggs 2002). Therefore for individually selected trees in need of protection, a novel mitigation method may prove more effective, here proposed the use of African honeybees (*Apis mellifera* subsp. *scutellata*).

African honeybees were first used as a mitigation method to deter elephants from impacting fever trees (*Vachellia xanthophloea* P. Hurter) Benth. in Kenya, where the presence of single beehives, especially active beehives, provided the trees with protection against elephant impact (Vollrath and Douglas-Hamilton 2002). The African honeybee is a particularly aggressive honeybee species (Alaux *et al*. 2009), and the stings of a swarming colony is hypothesised to pose a threat to vulnerable sensitive areas of an elephant, including behind the ears, around the eyes, and within and under the trunk (Vollrath and Douglas-Hamilton 2002). Subsequent studies have provided evidence that elephants display a variety of alarmed behaviours to the pre-recorded sounds of “buzzing” African honeybees (King *et al*. 2007), where the elephants produced distinctive “rumble” vocalisations in the process (King *et al*. 2010). African honeybees have further been used to successfully deter elephants from crop raiding through the design of beehive fence-lines, which consists of both active and inactive beehives connected to one another by wires and situated along the perimeter of crop fields (King *et al*. 2009; 2011). Most recently, it has been found that the West African honeybee (*A. m.* subsp. *adansonii*) can be used to protect fruiting trees from impact by forest African elephants (*L. cyclotis*) in Gabon (Ngama *et al*. 2016). However, it has yet to be determined whether African honeybees can be used to protect trees from elephant impact in enclosed reserves in South Africa, and in particular, protect a tree as highly sought after by elephants such as the marula tree. Therefore, this study’s objectives were (i) to test whether the presence of beehives in marula trees influenced the likelihood of the tree receiving elephant impact and compare these results to wire-netted trees; (ii) to assess if elephants avoided areas with marula trees containing beehives; and (iii) to provide a comparison of the financial costs associated with the beehive and wire-netting mitigation methods. I predicted that the beehive trees would be least impacted by elephants in comparison to wire-netted and control trees, as elephants should avoid trees containing beehives (Vollrath and Douglas-Hamilton 2002; King *et al*. 2011). However, wire-netted trees would still be efficient at preventing bark-stripping (Derham *et al*. 2016). I predicted that the presence of beehives would not result in the complete avoidance of an area by elephants, as elephants have still been recorded approaching beehives within a few metres (Karidozo and Osborn 2005; King *et al*. 2011). Considering the high costs and maintenance required for the beehive mitigation method in comparison to wire-netting, I expect that the beehive mitigation method will be most effective as a small-scale protection method, whilst wire-netting would be more successful as a large-scale mitigation method. However, the scale of usage will be dependent on the protected areas resources and willingness to implement and sustain the beehive mitigation method.

Materials and methods

Study area

This study was conducted in Jejane Private Nature Reserve (JPNR), a 21 km² protected area situated in the southern region of Balule Nature Reserve, part of the Greater KNP (Figure 1). JPNR was selected as an ideal study site because of its high density of adult marula trees (Helm and Witkowski 2012), and because elephants had been absent from the JPNR area of Greater KNP for over 100 years (G. Thomson, personal communication, November 23, 2016). JPNR receives a mean annual rainfall of 400 - 600 mm (G. Thomson, personal communication, February 21, 2016) and is located in the Granite Lowveld vegetation unit (SVI 3) in the Savanna biome (Mucina and Rutherford 2006). This vegetation unit is a moderately open savanna which is dominated by tall tree species such as *Sclerocarya birrea*, *Combretum apiculatum* Sond. and *Senegalia nigrescens* Oliv. (Peel *et al*. 1993; Mucina and Rutherford 2006). A study site of 30 ha (0.3 km²) was selected within the boundaries of JPNR (S24.29936; E30.98157). The study site was > 500 m away from any neighbouring properties and shareholder units to ensure that all residential units were at a safe distance from active beehives.

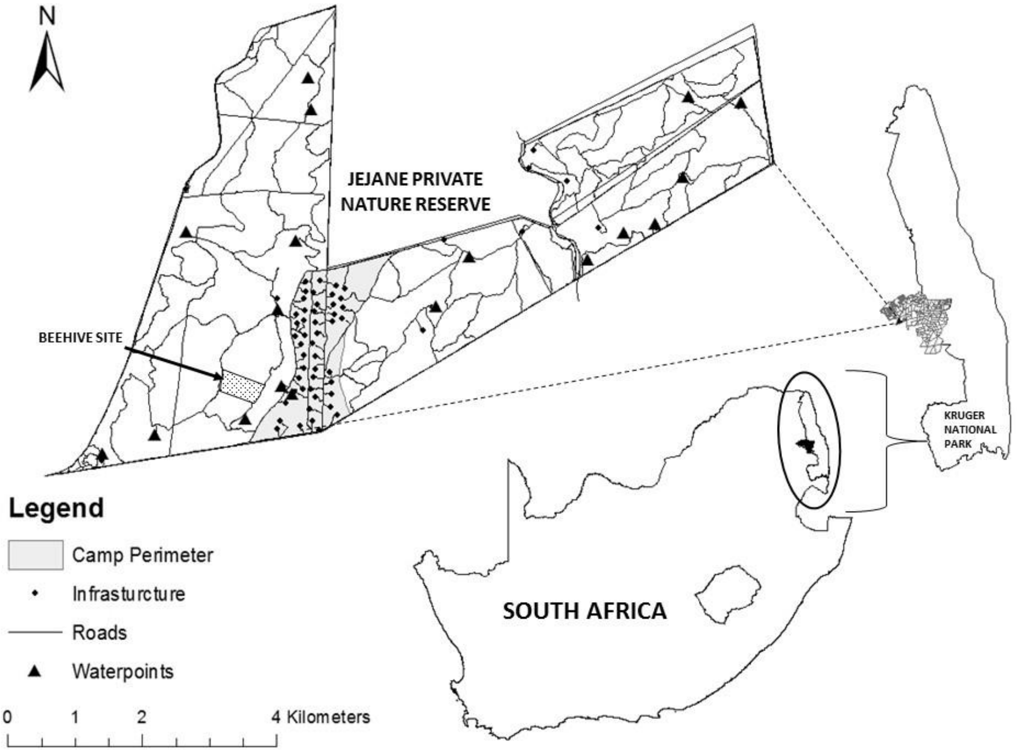

Figure 1: Location of Jejane Private Nature Reserve (JPNR) within the Greater Kruger National Park. The beehive study site was situated in the western section of JPNR, > 500 m from any human settlements.

Baseline elephant impact assessments

Baseline elephant impact assessments were carried out on 150 marula trees prior to the adoption of mitigation methods and the following elephant impact assessment methods adapted from Henley (2013). Only marula trees further than 15 m from a road were selected to avoid the effect of roads on a tree's susceptibility to elephant impact (Coetzee *et al*. 1979; Smit and Asner 2012). Marula trees which had previously been uprooted or had their main stem snapped were not included. Selected trees were > 7 m apart (main stem to main stem) to safely 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 as close as 1 - 2 m in Kenya; King *et al*. 2011).

Each marula tree was labelled by hammering a washer into the tree at breast height and recording the label number on a datasheet. Each tree's location was georeferenced using a Global Positioning System (GPS). The following measurements were recorded on each tree: the stem diameter at breast height (DBH) in cm; the height of each tree grouped into two height classes using the *VolCalc* digital photography method for estimating tree dimensions (Barrett and Brown 2012): Class 1 (5 - 8 m), and Class 2 (8 - 11 m). Because marula trees are dioecious, the sex of each tree was determined by searching for fruit endocarps below the tree’s canopy (Helm *et al*. 2009; Helm *et al*. 2011). Trees with endocarps underneath the canopy were classified as female trees. The following impact-types, as defined by Walker (1986) and modified by Greyling (2004) and Henley (2013), were assessed on each tree using the tree-fate classes described in Table 1: (1) bark-stripping, measured as the percentage of the main stem circumference that has been stripped of bark; and (2) primary branch breakage, which is the proportion of primary branches that have been broken off the tree. (Table 1). Uprooting, main stem snapping, and secondary branch breakage were assessed during post-baseline assessments (see *Elephant impact and mitigation efficiency* section).

Table 1: Elephant impact-types and tree-fate classes. Bark-stripping and primary branch breakage were assessed during the baseline assessment, as well as during post-baseline assessments. Uprooting, main stem snapping and secondary branch breakage were only assessed during post-baseline assessments.

Impact-type	**Tree-fate classes**									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Bark-stripping	No damage	< 1%	1 - 4%	5 - 10%	11 - 25%	26 - 50%	51 - 75%	76 - 90%	91 - 99%	100%
Primary branch breakage	No damage	> 0 - 25%	26 - 50%	51 - 99%	100%					
Uprooting	No damage	Tree alive, roots in ground, just leaning over	Tree pushed onto ground but is alive and has all roots in ground	Tree alive but has half of the roots in the ground and half of the roots exposed in the air	Tree has been uprooted (all of the tree's roots are in the air)					
Main stem snapping	No damage	Crown of tree is still attached to the main stem and the tree is still alive	Tree has subsequently died from main stem breakage							
Secondary branch breakage	No damage since baseline assessment	New damage since baseline assessment								

Mitigation methods

The 150 marula trees were divided into 50 groups of three trees (each group = one beehive tree; one wire-netted tree; and one control tree in a block design). The range in marula tree heights (class 1: > 5 - 8m; class 2: > 8 - 11 m) were distributed proportionately across the three mitigation methods to avoid bias in the probability of a height class being preferred by elephants (*ANOVA*: $F_{2,147} = 0.54$, $p = 0.58$, $n = 150$).

Beehives

One hundred beehives were built in the form of modified bait hives to be hung from the 50 beehive trees (Figure 2A and B). Each beehive tree had one active beehive (frames supporting a live honeybee colony) and one dummy beehive (empty box) (Figure 2C). As elephants will still approach a beehive within a couple metres (1 - 2 m; King *et al*. 2011), there is still a likelihood that elephants could impact the opposite side of a marula tree. Furthermore, the use of only dummy beehives in trees provides limited protection against elephant impact (see Vollrath and Douglas-Hamilton 2002). Therefore, given the costs associated with active beehives, our design aimed to test if elephants would still impact a marula tree if 1 beehive was active and the other beehive was a dummy beehive, since that would provide the same benefits of two active beehives and reduce the setup costs.

Figure 2: Beehive design - **(A)** All 100 beehives (50 active beehives and 50 dummy beehives) were built from 20 mm laminated pine shelving wood. The 50 active beehives and 50 dummy beehives were coated twice with *Waksol*, a solvent-based wax preservative for wood. Two handles were placed along the top sides of each beehive with holes drilled into the ends so that cable ties could be threaded through them. On the two shorter sides of each beehive, two holes (10 mm diameter) were drilled 100 mm from the top to serve as ventilation holes, whilst an entrance opening of 90 mm x 10 mm was cut into the bottom of the pine shelving wood. **(B and C)** Each beehive tree had two beehives hung from its branches on either side of the main stem. One of the two beehives was an active beehive, whilst the other beehive was a dummy beehive. In preparation for hanging the beehives, two nylon ropes with looped-ends were hung and stapled from each branch (± 50 cm apart) so that the looped-ends were 2 m above the ground (adult elephant eyelevel). One insulation lambdaboard was then placed on the roof of each active beehive. The hanging-design of the beehives from the branches meant that any major disturbances to the tree would result in the swaying of the beehives, thereby purposely disturbing the honeybees.

In preparation for hanging the beehives, nylon ropes were hung from the 50 beehives trees from 21 - 23 November, 2015. The 50 dummy beehives were connected to the ropes from 27 - 29 November, 2015, by connecting two cable ties between each nylon rope's looped-end and each corner of the dummy beehive (Figure 2B). Fifty African honeybee colonies were then brought into JPNR by a professional bee-keeping organisation and had their frames transferred into the 50 active beehives. The 50 active beehives were hung overnight (10 pm - 5 am) from 13 - 14 December, 2015, so that each beehive tree had one active beehive and one dummy beehive (Figure 2C). Initially, engine grease was smeared along the nylon ropes to prevent ants from raiding beehives, as is used on the wires in the Kenyan beehive fence-lines (L. King, personal communication, November 19, 2015). However, after ants raided six active beehives within the first two months post-hanging, a new product, *Plantex* glue, was spread on each of the hanging ropes over a distance of ± 20 cm

(March 01, 2016). No beehives were raided by ants after the *Plantex* was used, although some nylon ropes needed a second layer after six months.

The presence or absence of honeybee colonies within the beehives was assessed on a weekly basis (December 15, 2015 - September 28, 2016). If colonies had abandoned the beehives, then the possible source of abandonment was assessed. This included the invasion of ants into the beehives, or colonies vacating beehives for unknown reasons. Any irregularities on the beehives were immediately addressed in the field. A feeding regime for the honeybee colonies was implemented to supplement the colonies during the prevalent drought conditions of 2015 - 2016 in South Africa. Sixteen feeder stations were built and placed within the study site in January, 2016, providing the surrounding honeybee colonies with sugar water (ratio 1:3) through a drip system. All feeder stations were refilled every three days. As of May 30, 2016, a specialised nectar feed solution (*Nectar Feed*) was added to the sugar water to provide a nectar supplement during the winter months. A pollen substitute (*Protein Feed*) was simultaneously given to each active colony once a week (see *Booster Bee* products http://www.beequip.co.za/?page_id=101). Feeder station locations were changed in accordance to which beehives were still active, or if feeder stations were continually attacked by animals in a specific location.

Wire-netting

Chicken-mesh (13 mm, 1.8 m tall) was wrapped around the main stems of 50 marula trees, ± 50 cm off the ground and to a height of ± 230 cm (Figure 3). For each tree, the chicken-mesh was wrapped around the main stem twice to ensure that a rigid cage-like structure surrounded the main stem, whilst still permitting the main stem growth space. The ends of the chicken-mesh were stapled to the tree trunk using 25 mm wire-fencing staples. All 50 trees were covered with chicken-mesh within the period of a week (31 October, 2015 - 07 November, 2015).

Figure 3: Chicken-mesh (13 mm) wrapped around the main stem of a marula tree to protect the tree from bark-stripping by elephants. The chicken-mesh is wrapped around the main stem twice, creating a rigid cage-like structure, whilst allowing room for main stem growth.

Elephant impact and mitigation efficiency

Elephant impact on the 150 marula trees was monitored on a monthly basis (January - December, 2016) to record changes to the baseline elephant tree-fate classes for bark-stripping and primary branch breakage. Any changes to these tree-fate classes were recorded (Table 1). Uprooting, main stem snapping, and secondary branch breakage were also recorded during this period.

To determine whether the mitigation method affected the likelihood (presence/absence) of a tree receiving (1) elephant impact (any form of impact), (2) bark-stripping only, or (3) branch breakage only (primary and secondary branch breakage), log linear analyses were performed through a generalised linear model with a binomial distribution and a logit-link function. Tree height is known to affect a tree's susceptibility to elephant impact and was used as a second explanatory variable in the log linear analyses. Pearson's chi-squared tests of independence and post-hoc pairwise chi-square tests of independence were used to further investigate differences between mitigation methods and height categories using the *rcompanion* package (Mangiafico 2015). As female marula trees are more susceptible to elephant impact (Hemborg and Bond 2007), a Pearson's chi-square test of independence was used to determine if there was a significant difference between the number of male and female marula trees impacted by elephants. Weighted average impact scores for each tree were individually calculated for bark-stripping, primary branch breakage and secondary branch breakage. These were calculated using the mean number of trees per tree-fate class for each mitigation method (Table 1). Wilcoxon signed-rank tests were used to assess changes in weighted average impact scores between the baseline assessment and September 2016 assessment for the three impact-types (bark-stripping, primary branch breakage, secondary branch breakage) within each mitigation method. Tree height selection by elephants was assessed using preference ratios (Petrides 1975) to identify if elephants were targeting a specific height class. All statistical analyses were performed using R statistical software (R v. 3.2.2) with a significance level of 0.05 (R Core Team 2016).

Elephant dung transects

Dung transects were carried out once a week from January, 2016 - September, 2016 to compare elephant presence in the beehive site versus elephant presence in a control site directly north in the same road loop in JPNR (Figure 4). A total of six transects (300 m x 40 m) were set within the beehive site at a distance of 150 m from each other, whilst six replica transects were set in the control site. Each transect had a searching time of 15 minutes, where the GPS co-ordinates of any new elephant dung piles were recorded within each transect. Collective piles of dung by breeding herds or coalitions of bulls were treated as one dung sighting. Dung from breeding herds and bulls were not separated in the analysis as a breeding herd only moved through the combined sites once. A two-sample t-test was used to assess differences between the collective mean number of monthly dung sample sightings within the beehive and control sites' transects.

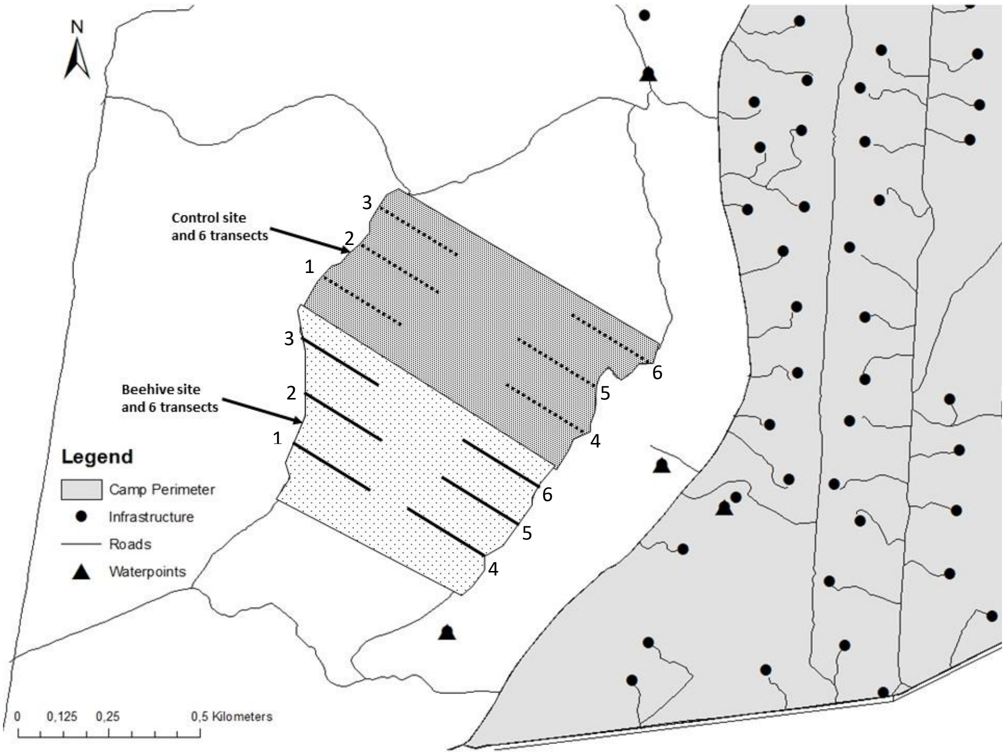

Figure 4: Elephant dung transects carried out in the beehive and control sites in Jejane Private Nature Reserve. Solid and dashed lines represent transects in the beehive and control sites, respectively. Each transect was 300 m x 40 m, with a search effort of 15 minutes.

Financial costs comparisons

Financial costs were compared between the beehive and wire-netting mitigation methods. Costs were calculated on an individual tree basis. Costs were divided into *Setup costs* and *Additional running costs*. *Setup costs* included all construction expenses associated with each mitigation method (materials, labour), whilst *Additional running costs* included any further expenses once the mitigation method was setup. *Setup costs* for the wire-netting included the chicken-mesh, staples and labour. *Setup costs* for the beehives included the beehive materials and manufacturing labour (Figure 2A), the materials required for hanging the beehives (Figure 2B and C), and the purchasing of one live honeybee colony per beehive tree. There were no *Additional running costs* for the wire-netting. The costs of sugar for sugar water, as well as nectar and pollen substitute, were calculated on a monthly basis as *Additional running costs* for the beehive mitigation method and were divided by the number of beehive trees. Financial costs were then estimated for a 10-year period to investigate the longevity-financial relationship of the mitigation methods. Financial costs excluded interest rate increases and were calculated on a Rand-Dollar exchange rate of R13.42 for US $1. For beehive *Setup costs*, it was estimated that the wooden beehives would need replacing every two years (Kalnins and Erickson 1986), and so construction costs were multiplied by five over a ten year period. The active honeybee colony would be transferred into the new beehive. For wire-netting, it was estimated that the chicken-mesh would need replacing once every ten years, and so wire-netting costs were doubled for a 10-year period.

Ethical clearance

This study was approved by the Animal Ethics Screening Committee of the University of Witwatersrand, Johannesburg (AESC 2015/07/26/0).

Results

Beehive occupancy

Of the 50 active beehives at the start of the study period, 26 beehives were abandoned within the first half of the study period (4½ months) as a result of ant invasions or possible external factors related to the drought (Figure 5). Active beehive numbers stabilised within the second half of the study period with the addition of nectar and pollen substitute into the feeding regime from 30 May, 2016. In June 2016, one dummy beehive was colonised by a wild swarm (Figure 5). The active beehive on the opposite side of this tree had previously been abandoned.

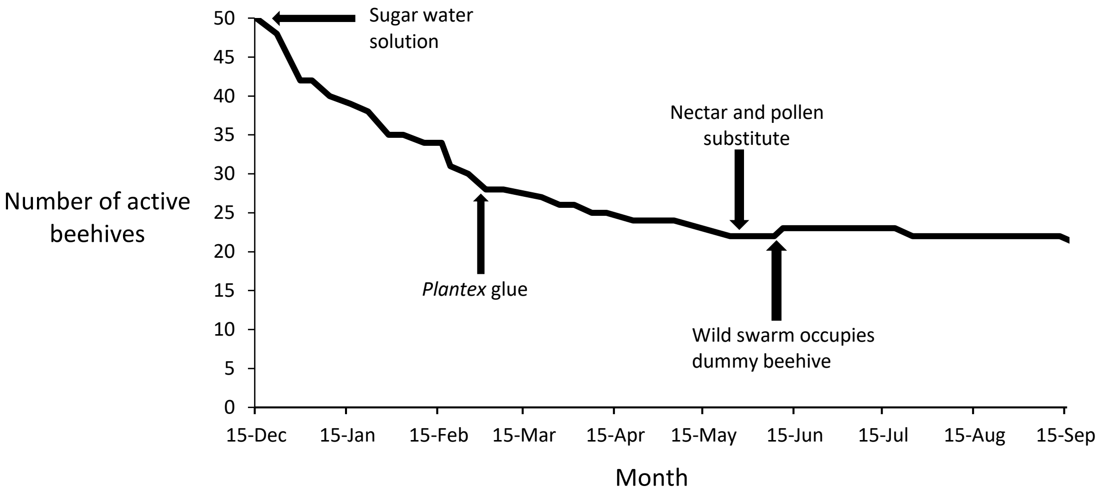

Figure 5: Number of active beehive colonies during the study period in Jejane Private Nature Reserve. The number of active beehive colonies stabilised after the addition of nectar and pollen substitute into the feeding regime. Ants resulted in 24% (n = 7) of beehive abandonments by honeybee colonies.

Elephant impact and mitigation method efficiency

Impact (all impact-types)

The number of trees receiving new impact by elephants differed significantly between the mitigation methods ($\chi^2_2 = 33.53$; $p < 0.0001$; $n = 150$), with the number of control trees impacted on by elephants (n = 27) significantly higher than the number of wire-netted (pairwise chi-square tests of independence: $n = 14$, $p < 0.05$) and beehive trees (pairwise chi-square tests of independence: n = 1, $p < 0.0001$, Figure 6). The only beehive tree to receive elephant impact had secondary branches broken (Figure 6, Table 2). 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 5 for primary branch breakage). No heavy impact (> 50% for bark-stripping and primary branch breakage) was recorded on wire-netted and beehive trees. Tree height was a significant determinant of a tree receiving elephant impact (log linear analyses: $p < 0.01$), with elephants showing a greater preference for trees in height class 1 (5 - 8 m) (preference ratio: 1.31) in comparison to height class 2 (8 - 11 m) (preference ratio: 0.65) ($\chi^2_1 = 6.05$; $p < 0.05$; $n = 150$, Figure 7). Height class preference for elephants did not differ between mitigation methods (Figure 7). The number of female trees receiving impact (25 of 123) was significantly less than the number of male trees (17 of 27) ($\chi^2_1 = 19.97$; $p < 0.00001$; $n = 150$). However, as no fruit was recorded on the trees during the study period, and due to the low number of male trees in the site, the effect of sex on elephant impact was not investigated further.

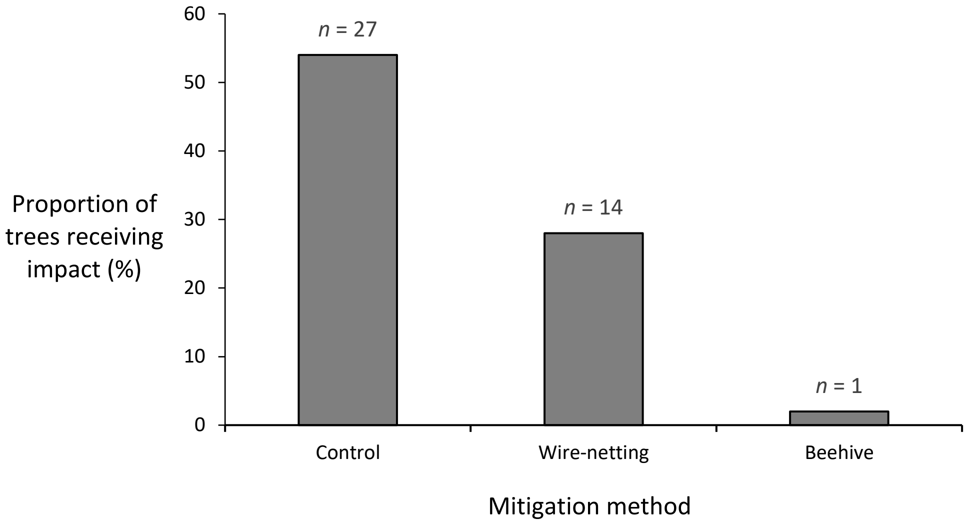

Figure 6: Proportion of marula trees per mitigation method receiving elephant impact in Jejane Private Nature Reserve. Elephant impact included bark-stripping, primary branch breakage, secondary branch breakage, and main stem snapping. No trees were uprooted during the study period. *n* = number of trees per mitigation method with new elephant impact.

Table 2: Number of marula trees receiving new elephant impact across the impact-types for the three mitigation methods in Jejane Private Nature Reserve.

Mitigation method	**Bark-stripping**	**Primary branch breakage**	**Secondary branch breakage**	**Main stem snapping**	**Uprooting**	**Total trees damaged**
Control	13	8	11	1	0	27
Wire-netting	0	1	13	0	0	14
Beehive	0	0	1	0	0	1

Bark-stripping

The number of trees receiving bark-stripping from elephants differed significantly between mitigation methods ($\chi^2_2 = 30.88$; $p < 0.0001$; $n = 150$), with the number of control trees bark-stripped (n = 13) significantly higher than wire-netted (pairwise chi-square tests of independence: n = 0, $p < 0.01$) and beehive trees (pairwise chi-square tests of independence: n = 0, $p < 0.01$, Table 2). Bark-stripping was the most common form of elephant impact on control trees (Table 2) and the weighted average impact score for bark-stripping on the control trees increased significantly over the 9-month study period (Wilcoxon signed-rank tests: $p < 0.01$, $n = 50$, Table 3).

Branch breakage

The number of trees receiving branch breakage differed significantly between mitigation methods ($\chi^2_2 = 16.92$; $p < 0.001$; $n = 150$), with the number of beehive trees with new broken branches (n = 1) significantly lower than wire-netted (pairwise chi-square tests of independence: n = 14, $p < 0.05$) and control trees (pairwise chi-square tests of independence: n = 19, $p < 0.01$, Table 2). There were significant increases in the weighted average tree-fate classes for both primary (Wilcoxon signed-rank tests: $p < 0.05$, $n = 50$, Table 3) and secondary (Wilcoxon signed-rank tests: $p < 0.01$, $n = 50$, Table 3) branch breakage of control trees, although only secondary branch breakage increased significantly for wire-netted trees (Wilcoxon signed-rank tests: $p < 0.01$, $n = 50$, Table 3). 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) ($\chi^2_1 = 4.03$; $p < 0.05$; $n = 150$).

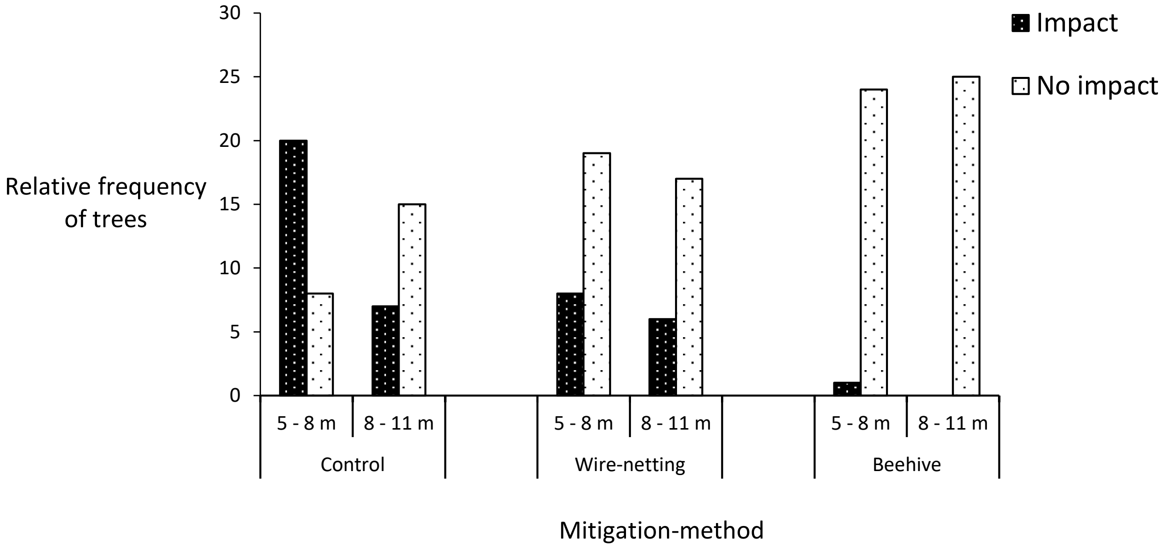

Figure 7: The relative frequency of marula trees impacted by elephants across height classes for mitigation method in Jejane Private Nature Reserve. Trees in height class 1 (5 - 8 m) were more vulnerable to elephant impact than trees in height class 2 (8 - 11 m) for all mitigation methods.

Table 3: Comparison of weighted average impact scores (mean ± S.E.) between the baseline assessment (October, 2015) and final assessment (September, 2016) in Jejane Private Nature Reserve. * $p < 0.05$; ** $p < 0.01$, NS = not significant.

Mitigation method	**Bark-stripping**		***p***	**Primary branch breakage**		***p***	**Secondary branch breakage**		***p***
	Baseline	**Final assessment**		**Baseline**	**Final assessment**		**Baseline**	**Final assessment**	
Control ($n = 50$)	1.50 ± 0.16	1.80 ± 0.18	**	1.16 ± 0.07	1.60 ± 0.18	*	1.00	1.22 ± 0.06	**
Wire-netting ($n = 50$)	1.72 ± 0.19	1.72 ± 0.19	NS	1.58 ± 0.14	1.62 ± 0.14	NS	1.00	1.26 ± 0.06	**
Beehive ($n = 50$)	2.08 ± 0.26	2.08 ± 0.26	NS	1.38 ± 0.11	1.38 ± 0.11	NS	1.00	1.02 ± 0.02	NS

Elephant dung transects

Elephants were similarly present in both the beehive and control site between January 13, 2016 and September 28, 2016 with a total of 43 dung sample sightings within the beehive site and 47 in the control site. There was no significant difference between the mean number of dung sample sightings per month in the beehive and control sites ($t_{(16)} = -0.28$; $p = 0.79$; $n = 9$).

Financial costs comparisons

A total of 68.91 m of chicken-mesh was used for the 50 wire-netted marula trees (per tree = 1.38 ± 0.23 m) at a mean cost of $10.50 per tree (Table 4). There were no *Additional running* costs for wire-netting. The beehive mitigation method was more expensive as the total cost of two beehives per tree (one active beehive and one dummy beehive) was $62.50, with an additional cost of $27.75 for the purchase of a live African honeybee colony. As the honeybee colonies required sugar water, as well as nectar and pollen substitute during the drought, there were further additional costs per tree (Table 4). The 10-year estimate construction costs reflect the wooden beehives being replaced every two years and the wire-netting being replaced once in a 10-year period (Table 4). The 10-year estimated costs for wire-netting may be an over-estimate though, as wire-netted trees in the Greater KNP have lasted at least ten years if the construction was implemented correctly (M. Henley, personal communication, February 06, 2017).

Table 4: Comparison of the financial costs per tree (Dollars and Rands) for using the beehive and wire-netting elephant mitigation methods. Costs are calculated over one- year and ten- year periods.

Mitigation method	**Time scale**	**Setup**		**Set up cost per tree**	**Additional running costs**		**Total overall cost per tree**
		Construction	**Honeybee colony**		**Sugar water per tree**	**Nectar and pollen substitute per tree**	
Beehive tree	*1 year estimate per tree*	$62.50 (R850)	$27.75 (R350)	**$90.25 (R1,200)**	$18 (R240)	$31 (R420)	**$229.50 (R3,060)**
	10 year estimate per tree	$312.50 (R4,250)	$27.75 (R350)	**$340.25 (R4,600)**	$180 (R2,400)	$310 (4,200)	**$1,170.50 (R15,800)**
Wire-netted tree	*1 year estimate per tree*	$10.50 (R140.92)	-	**$10.50 (R140.92)**	-	-	**$10.50 (R140.92)**
	10 year estimate per tree	$21 (R281.84)	-	**$21 (R281.84)**	-	-	**$21 (R281.84)**

Discussion

Elephant impact and mitigation method efficiency

New elephant impact was recorded on 27 control trees, 14 wire-netted trees and 1 beehive tree. The only beehive tree to receive elephant impact had secondary branches broken, in which the dummy beehive was pulled out of the tree. The wire-netting prevented bark-stripping but was still susceptible to branch breakage.

This is the first known study in South Africa to use beehives as a mitigation method for elephant impact on marula trees and the results suggest that elephants avoided impacting these trees, regardless of beehive occupancy. In the original elephant-bee experiments by Vollrath and Douglas-Hamilton (2002), 24 out of the 30 *V. xanthophloea* trees with inactive beehives received some form of elephant impact, whilst none of the six trees with active beehives were impacted. This current study provides evidence that beehives can be highly successful in mitigating elephant impact. King *et al*. (2011; 2017) found that the combination of active and inactive beehives in a beehive fence-line could successfully deter elephants from crop raiding, which suggests that as long as dummy beehives are combined with active beehives in a mitigation-setup, they can be used effectively to deter elephants. The lack of impact on trees with both a dummy beehive and inactive beehive (active beehive which had been abandoned by the colony), suggests that a combination of the smell from the inactive beehive and the swinging motion of both beehives in the tree was still sufficient in mitigating elephant impact. However, it is unknown as to whether the mere presence of the beehives in the tree or the pheromones alone repel the elephants. Elephants have a well-developed sense of smell (Laws 1970) which may deter them from approaching and disturbing trees containing beehives, even if the beehive has been previously abandoned. Furthermore, active beehives were prone to producing loud “buzzing” sounds when disturbed by gusts of wind or physical handling, which would cause the beehives to sway in the trees (personal observation). Elephants have acute hearing capabilities (Hefner and Hefner 1980) and respond to the playback recordings of “buzzing” honeybees by moving away from the sound source (King *et al*. 2007; 2010). The only beehive tree to receive elephant impact had some of its secondary branches broken off and the dummy beehive had been ripped out of the tree onto the ground. Tracks of a large elephant bull were found 3 m from the tree’s main stem. Interestingly, this impact took place on a tree with an active beehive on the other side of the main stem. Elephants have previously been recorded damaging unoccupied beehives in trees (Karidozo and Osborn 2005) and it was noted that an elephant bull in musth was recorded in the JPNR beehive site three days after the incident (personal observation). Musth bulls are aggressive by nature (Poole and Moss 1981) and their reaction to a beehive may be different when in this intensified state (Midgley *et al*. 2005). As this was the first year that this experiment was carried out on elephants in JPNR, it still remains to be seen if other elephants will begin to learn that the dummy beehive-side of a tree is safe to forage if the active beehive is not disturbed, or that a tree with two inactive beehives does not pose a physical threat (Karidozo and Osborn 2005; King *et al*. 2007).

Wire-netting was successful at preventing bark-stripping from elephants. Bark-stripping was the most common form of elephant impact on the control trees which provides support for the effectiveness of wire-netting as a mitigation method for bark-stripping. During a nine-year study on wire-netted trees in the Greater KNP, only 1.7% of trees had been bark-stripped, of which none had been ring-barked (Derham *et al*. 2016). Although elephants may be able to challenge wire-netting by placing their tusks through the chicken-mesh and ripping it off (Henley 2013), this is more difficult to do when the chicken-mesh diameters are small and more difficult for an elephant’s tusk to penetrate. One wire-netted tree used as a rubbing post by an elephant during this study, evident by the mud smeared along the chicken-mesh. It has not yet been tested whether the uneven surface of the wire-netting makes it an attractive rubbing surface for elephants. Wire-netted trees were, however, still vulnerable to primary and secondary branch breakage and tree felling. Of the trees surveyed by Derham *et al*. (2016), 64% had received primary branch breakage, whilst 7% of the trees had been main stem snapped. As there is no immediate danger to elephants from wire-netting, wire-netted trees are still susceptible to all other forms of elephant impact. (Grant *et al*. 2008; Henley 2013; Derham *et al*. 2016), as well as secondary effects from woodborers (Coetzee *et al*. 1979).

Elephant dung transects

There was no significant difference in the quantity of elephant dung sightings between the beehive and control sites. The presence of beehives, therefore, even at the high densities in this study (21 - 50 active colonies in 30 ha), did not prevent elephant presence within the beehive site. This suggests that the presence of beehives only has a disturbance effect on elephants, resulting in the elephants avoiding particular trees. Elephants have been recorded moving along beehive fence-lines within 1 - 2 m (King *et al*. 2011) and have inflicted heavy impact on trees within 5 m of active and inactive beehives (Karidozo and Osborn 2005). Control and wire-netted trees that were in close proximity to beehive trees in this study were still vulnerable to elephant impact. However, spatial distances to elephants may vary in accordance to the activity levels of the beehive (Ngama *et al*. 2016). A beehive colony's defence levels are positively correlated with its activity levels (Woyke 1992), and elephants appear to avoid beehives with high activity levels (Ngama *et al*. 2016). Whilst beehive activity levels were not measured in this current study, it is possible that an active beehive's ability to protect a tree and affect elephant spatial movement is dependent on the activity and defence levels of the particular colony. As the African honeybee alarm pheromones have recently been analysed in detail (Nouvian *et al*. 2016), the possibility also 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. These possibilities require further investigation in future studies as they have financial implications regarding the reduction of the number of active beehives required over large areas for positive reinforcement.

Financial costs comparisons

The setup cost of placing an active and dummy beehive in a tree was $90.25, far greater than the cost of wire-netting ($10.50 per tree). Beehives also have additional feeding costs if floral resources are low. These financial costs were calculated using the total costs of 50 trees per mitigation method and so individual tree prices may be slightly higher. The differences in the financial costs of the beehive and wire-netting mitigation methods, as well as how successful each method is against elephant impact, necessitates a managerial trade-off between the two mitigation methods. On the positive side beehives are effective against all forms of elephant impact and active beehives can also produce honey that can be sold to offset part of the costs or as financial revenue for the protected area or community involved in the beehive mitigation method. This financial system has been implemented in Kenya where farmers benefit from the income from harvested 'elephant friendly' honey (King *et al*. 2009; 2011; 2017). African honeybees also provide pollination services to many savanna trees, including marula trees (Leakey *et al*. 2005; Chirwa and Akinnifesi 2008). On the negative side, the beehive mitigation method is labour intensive with maintenance required for the condition of the beehives, reapplying of *Plantex* glue on the nylon ropes, and potentially feeding the honeybees. Wooden beehives also need to be replaced every few years because of warping, water absorption and insect attack (Kalnins and Erickson 1986). The use of modern wood-free beehives, although initially more expensive than wooden beehives, would help reduce costs over time (see *The BeePak* design http://beepakworld.com). Beehives in trees may also be aesthetically unpleasing to tourists and dangerous if disturbed. Careful planning is therefore needed when deciding on where to place beehives in protected areas. Furthermore, trees that are designated for the beehive mitigation method should not be in areas where fire burn practices are regularly carried out, or in the vicinity of electric fences and pylons, as this could result in the honeybees absconding from the beehive or the beehive being destroyed in the fire itself (Wellenstein 1973; Hepburn 2006).

Wire-netting is a cheaper mitigation method and requires very little maintenance once installed. Derham *et al*. (2016) reported wire-netting on trees in the Greater KNP lasting at least nine years and the longevity of the wire-netting may be dependent on external factors such as (1) elephants rubbing against wire-netted trees and weakening the chicken-mesh, (2) chacma baboon (*Papio ursinus*) climbing on the chicken-mesh and pulling out the staples, or (3) the setting up of the chicken-mesh around the tree is not executed thoroughly (M. Henley, personal communication, February 06, 2017). Continuous exposure to fire may also weaken the chicken-mesh overtime, and wire-netted trees may still be exposed to secondary effects of woodborer invasions as a result of previous elephant impact (Coetzee *et al*. 1979).

The low costs and relative lack of maintenance required for wire-netting suggests that this elephant mitigation method would be highly efficient for large-scale usage, increasing the survival rates of large trees across a large protected area (Henley 2013). The higher financial costs and greater maintenance required for the beehives may limit this mitigation method to small-scale usage for selectively important trees in protected areas and would be more successful if associated with a financial revenue scheme from the harvested honey.

Conclusion

This study aimed to assess the effectiveness of beehives as a mitigation method for elephant impact on marula trees and compare its effectiveness to wire-netting. Initial findings indicate that whilst wire-netting is a cheaper mitigation method and requires less maintenance, beehives offer greater protection against all forms of elephant impact on trees. The high maintenance and costs limits beehives to small-scale usage as a mitigation method, but harvested honey may bring in additional financial revenue for the protected area. Furthermore, investigations into the use of African honeybee pheromones and longer-lasting beehives will help reduce the associated costs of the beehive mitigation method. The results of this study illustrate that African honeybees can be used as an effective non-lethal mitigation method for elephant impact on marula trees, although logistical investment will be dependent on the financial and logistical resources available to the protected area.

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Chapter 4

Synthesis and discussion

General overview

Concerns have been raised over the impacts that high densities of African elephants (*Loxodonta africana* Blumenbach 1797) have on vegetation structure and biodiversity in enclosed protected areas (Birkett 2002; Asner *et al*. 2015). Long-term tree studies in South Africa's Greater Kruger National Park (Greater KNP) have recorded significant declines in the densities of large trees across the Greater KNP (Whyte *et al*. 2003; Asner *et al*. 2015). Elephants have a particular preference for marula (*Sclerocarya birrea* (A. Richard) Hochst. subsp. *caffra* (Sond.) Kokwaro (Anacardiaceae)), with severe bark-stripping, branch breakage, stem snapping and uprooting recorded on trees across the Greater KNP (Jacobs and Biggs 2002; Helm *et al*. 2009; Henley 2013; Helm and Witkowski 2013). Another concern for marula populations is a lack of recruitment in some areas, where high levels of seed predation (Helm *et al*. 2011a), fires (Jacobs and Biggs 2001; Helm *et al*. 2011b), and herbivory on seedlings (Lewis 1987; Haig 1999) can result in adult-dominated populations (Helm and Witkowski 2012). Populations that experience such bottlenecks at the seed and seedling levels are potentially proceeding towards local extirpation (O'Connor *et al*. 2007).

The current scientific paradigm in South Africa focuses on managing the impacts and effects of species, rather than species numbers alone (Owen-Smith *et al*. 2006; Ferreira *et al*. 2011). Novel methods are therefore required to mitigate elephant impact on large trees such as marula. This study assessed elephant impact on marula trees in Jejane Private Nature Reserve (JPNR), a protected area within Greater KNP which had not had elephants present in over 100 years. A previous assessment found that JPNR had an adult-dominated marula population prior to the migration of elephants due to fence removal (Helm and Witkowski 2012) and therefore marula seed predation was assessed in this study in conjunction with elephant impact (Chapter 2). Lastly, as African honeybees (*Apis mellifera scutellata*) have been successfully used to deter elephants from trees (Vollrath and Douglas-Hamilton 2002) and crop-fields (King *et al*. 2011; 2017) in Kenya, the mitigation method of hanging active and dummy beehives in marula trees was tested in JPNR (Chapter 3). These results were compared to a currently used elephant mitigation method, wire-netting (see Derham *et al*. 2016). This synthesis aims to draw conclusions from the previous research chapters on elephant-marula tree interactions in JPNR and provide recommendations towards the future of beehives as a mitigation method in South Africa.

Marula population dynamics in Jejane Private Nature Reserve

The JPNR marula population surveyed in 2009 by Helm and Witkowski (2012) had declined by 23.8% in 2016 and still displayed an adult-dominated population (Chapter 2). Only two seedlings were found and 84.2% of the sampled marula endocarps had seeds missing from locules (Chapter 2). As JPNR had an adult-dominated marula population prior to the migration of elephants in 2013, it is necessary to focus on factors, aside from elephants, that are preventing seeds from establishing into seedlings, as well as seedlings from establishing into saplings and adult trees. The high seed predation levels may be indicative of rodent predation (Midgley *et al*. 2012), as rodent numbers are high in unburnt savannas (MacFadyen *et al*. 2012). Trees squirrels (*Paraxerus cepapi*) have a particular preference for marula seeds and act both as seed predators and dispersal agents (Midgley *et al*. 2012). The lack of marula seedlings in JPNR cannot be attributed to fire (Jacobs and Biggs 2001; Helm *et al*. 2011b), as no fires have occurred in the JPNR area since the year 2000 (G. Thomson, personal communication, January 10, 2017). As discussed in Chapter 2, JPNR has a high impala (*Aepyceros melampus*) density relative to surrounding protected areas, and relatively high impala densities in JPNR (Spencer 2011; Ferreira *et al*. 2013) have been correlated with a decrease in seedling numbers (Lewis 1987; Skarpe *et al*. 2004; Moe *et al*. 2009). Furthermore, elephants show a high preference for the smaller height classes of adult marula trees (5 - 11 m; Chapter 2), which may further amplify the adult-dominated population structure in JPNR if no recruitment takes place. Whilst the rate of elephant impact on marula trees in JPNR may slow down over time, there is still increased emphasis on the need to protect the remaining adult marula trees.

Beehives as a mitigation method for elephant impact on marula trees

Beehives were highly effective at mitigating elephant impact on marula trees, with only one of the 50 beehive marula trees receiving elephant impact (Chapter 3). During this incident, the dummy beehive was knocked out of the tree onto the ground and secondary branches were broken on the tree (Chapter 3). Considering that 14 wire-netted trees and 27 control trees received elephant impact, albeit of a light- to moderate- for the former, and moderate- to heavy impact intensity for the latter (Chapter 3), the beehive mitigation method's efficiency suggests it can be added as a new management tool for protecting large trees in protected areas. Whilst beehives have been used to protect trees from elephant impact elsewhere in Africa (Vollrath and Douglas-Hamilton 2002; Karidozo and Osborn 2005; Ngama *et al*. 2016), this is the first known experiment on the use of African honeybees to protect marula trees from elephant impact in South Africa. Marula trees are highly sought after by elephants (Weaver 1995; Shannon *et al*. 2008; Henley 2013) and have been listed as a protected species in South Africa since 1962 (Shackleton and Shackleton 2005). Therefore conservation efforts are required for marula trees, both inside and outside of protected areas (Shackleton *et al*. 2003). The use of African honeybees provides managers with a method for managing elephant impact on selected marula trees without having to resort to lethal methods of controlling elephant numbers (Whyte *et al*. 1998) and is aligned with the *South African Elephant Research Strategy* (DEA 2013) and South African National Park's *Elephant Management Plan* (SANParks 2012) for managing elephant effects in protected areas. African honeybees are also important pollinators of marula trees (Leakey *et al*. 2005; Chirwa and Akinnifesi 2008) which is an added benefit towards implementing the beehive mitigation method.

The spatial effect that beehives have on elephant locations is also important to understand when implementing this mitigation method. The presence of both active and dummy beehives in marula trees did not deter elephants from moving through the beehive site, with elephants moving around beehive trees rather than avoiding the entire site (Chapter 3). Whilst beehive fence-lines in Kenya are successful at preventing elephants from entering crop-fields (King *et al*. 2009; 2011; 2017), the presence of beehives hanging from individual trees will not prevent elephants moving through an area if the elephants are not required to come into contact with the beehives. The managerial implications are such that the proposed beehive mitigation method in chapter 3 will be effective at mitigating elephant impact on an individual tree, but other fencing-methods may be required to protect larger parts of protected areas (see Grant *et al*. 2008). Beehives in trees should therefore be regarded as an elephant mitigation method for individual trees and not necessarily spatial areas.

Beehives versus wire-netting

The beehive mitigation method was more effective against elephant impact in comparison to wire-netting. In comparison, wire netting was far more cost effective than the use of beehives per tree (Chapter 3). As both mitigation methods can be used to protect individual trees from elephant impact, each mitigation method will depend on the quantity of trees in need of protection, the financial-status of the protected area, as well as available manual labour for the mitigation method setup and maintenance. Wire-netting has been successful in preventing bark-stripping by elephants (Derham *et al*. 2016; Chapter 3) and can increase the survival rate of tree populations over time (Henley 2013). The low maintenance required for wire-netting trees makes it a convenient method for managers to use on a large scale across protected areas. Wire-netted trees are, however, still susceptible to all other forms of elephant impact when tested over a wider area and for a longer period (Henley 2013; Derham *et al*. 2016; Chapter 3), as well as secondary attack from woodborers due to elephant impact (Coetzee *et al*. 1979). The beehive-mitigation is an expensive mitigation method with maintenance required more regularly than wire-netting. This mitigation method is, however, effective against all forms of elephant impact (Chapter 3). The beehive mitigation method may be a more preferable method for individually-selected trees in need of protection, whether for aesthetic-, economic- or tourism-related factors. There is also the financial income that can be generated through the selling of harvested honey, as has been done in Kenya from the beehive fence-lines (King *et al*. 2011).

Improvements to the beehive mitigation method and future research

The beehive mitigation method is largely successful on two levels: protecting resources from elephant impact and providing honey as a source of financial revenue (Vollrath and Douglas-Hamilton 2002; King *et al*. 2009; 2011; Chapter 3). In Kenya, log beehives from the original beehive fence-lines (King *et al*. 2009) were upgraded to Kenyan top-bar beehives to improve the honey quantity and quality (King *et al*. 2011). Beehives such as the Kenyan top-bar beehive, or the popular Langstroth beehive have queen excluders which separates the beehive into honey and brood chambers (Magnuson and Lundall-Magnuson 2001). As honey from natural beehives would usually be mixed with brood (Seeley and Morse 1976), these modern designs allow beekeepers to harvest a clean honey product (Magnuson and Lundall-Magnuson 2001). Although full-scale top-bar and Langstroth beehives may not be practical for hanging in trees, smaller adaptations of these beehives would increase the quality of honey that protected areas would be able to harvest and sell from the beehives. These beehives may also increase beehive colony size and therefore the beehive activity and defence levels (Ngama *et al*. 2016). Beehives that last longer in the field will also reduce the replacement costs overtime. New beehive designs, which are moving away from the traditional wooden properties, are expected to last longer against external environmental factors. Although the original setup costs may be higher for these beehives, their longevity will make them more affordable overtime for protected areas.

Whilst the beehive mitigation method was successful at mitigating elephant impact on marula trees (Chapter 3), further studies are required on its efficiency against impact on other sort-after or protected tree species. Of particular conservation concern is the baobab (*Adansonia digitata* L.) population in protected areas in South Africa (Edkins *et al*. 2008). However, the effectiveness of the current beehive mitigation method design from chapter 3 may not be sufficient at mitigating elephant impact on a tree with as large a main stem diameter as a baobab (up to 9 m, Coates Palgrave 2002). A new design consisting of three to four beehives, of which one is active, may be more appropriate for a tree of this size. It will therefore be important to try out various designs and arrangements of active and dummy beehives that will be suitable for the size of the tree from which the beehives will be hung. African honeybees also produce alarm pheromones (Nouvian *et al*. 2016), and the possibility exists that elephants can detect these pheromones and may respond similarly to the presence of active beehives. Further research into this phenomenon is required as it would reduce the costs involved from hanging and maintaining beehives in trees.

As briefly mentioned in Chapter 3, Ngama *et al*. (2016) found a negative correlation between the honeybee activity levels of West African honeybees' (*A*. *m*. subsp. *adansonii*) and the presence of forest African elephants *L*. *cyclotis* around these beehives. Replicating the Ngama *et al*. (2016) methods on the interaction between African honeybees and African elephants would provide valuable insight into the relationship between the two species, and could potentially explain why trees containing particular beehives may still be targeted by elephants. Honeybee colonies have distinct collective personalities, differing in behaviours such as foraging activities and defensive responses (Wray *et al*. 2011). These behavioural variations in honeybee colonies, combined with the behavioural variation observed amongst African elephant individuals (Wittemyer *et al*. 2007), could lead to promising studies into understanding the range of factors that influence the effectiveness of beehives against elephant impact.

Conclusion

This study assessed the marula population structure in JPNR after three years of exposure to elephants (Chapter 2). Furthermore, beehives were tested as a mitigation method for elephant impact on marula trees within JPNR and compared to the wire-netting mitigation method (Chapter 3). The non-invasive management strategies for marula trees in protected areas will be largely based on each protected area's objectives and values (Figure 1). These strategies exclude invasive elephant management strategies such as translocation, contraception and culling (SANParks 2012). Whilst fire regime management will affect the number of seedlings and saplings establishing into adult trees (Jacobs and Biggs 2001; Helm *et al*. 2011b), and a decreased surface water density may lower the number of impala and elephants in an area (Smit *et al*. 2007a and b), mitigation methods can also be used to protect large trees on an individual scale, thereby not only maintaining aesthetically important landscape features, but protecting valuable seed banks (Figure 1). The beehive and wire-netting mitigation methods provide conservation managers with non-lethal measures to protect large trees from elephant impact within protected areas and the usage of these methods will be dependent on the degree of tree protection required and the conservation objectives of the protected area.

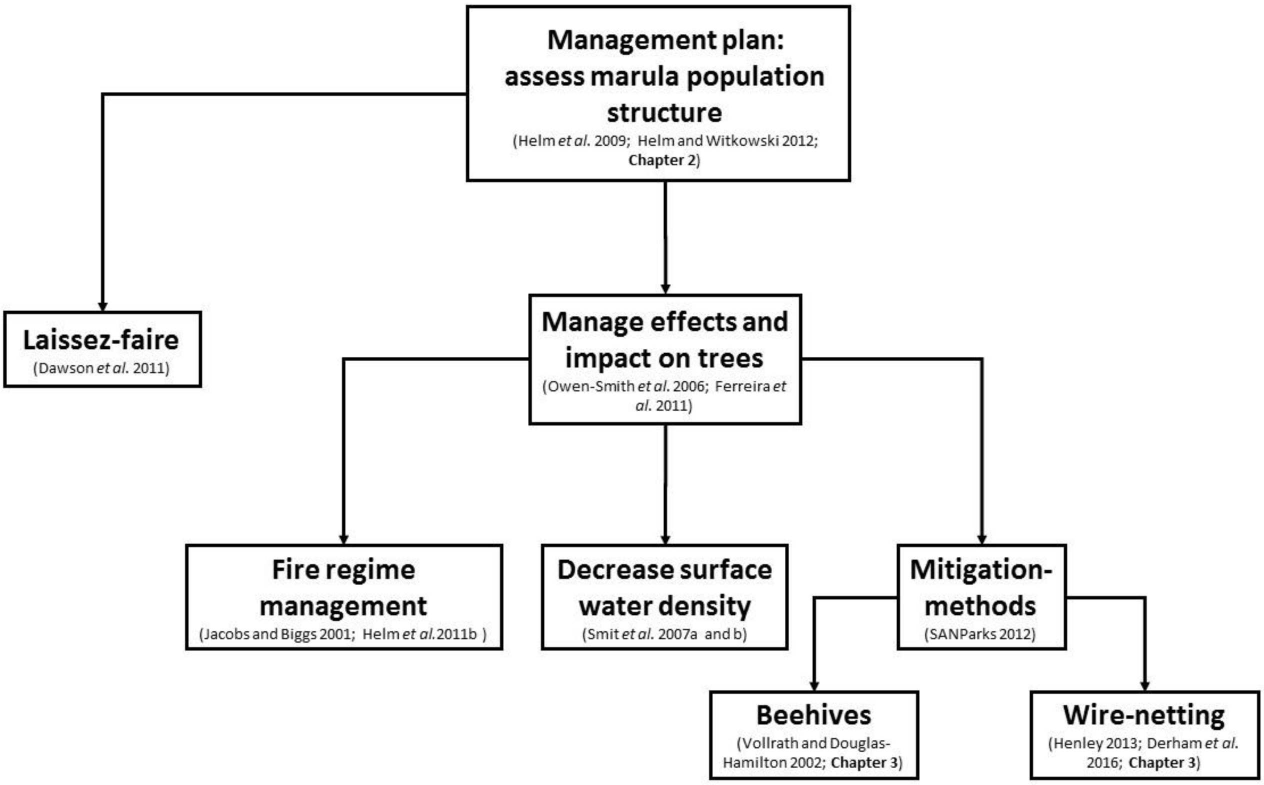

Figure 1: Non-invasive management strategies for marula tree conservation in protected areas in South Africa. Chapter 2 in this study assessed the marula population structure in Jejane Private Nature Reserve and Chapter 3 compared the effectiveness of beehives and wire-netting as mitigation methods for elephant impact on marula trees.

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