

XAOSIS

The management dilemma: Removing elephants to save large trees



Authors:

Michelle D. Henley^{1,2} Robin M. Cook²

Affiliations:

¹Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Pretoria, South Africa

²Elephants Alive, Hoedspruit, South Africa

Corresponding author:

Michelle Henley, michelephant@ savetheelephants.org

Dates:

Received: 20 Dec. 2018 Accepted: 16 May 2019 Published: 15 Aug. 2019

How to cite this article:

Henley, M.D. & Cook, R.M., 2019, 'The management dilemma: Removing elephants to save large trees', *Koedoe* 61(1), a1564. https://doi.org/10.4102/koedoe. v61i1.1564

Copyright:

© 2019. The Authors. Licensee: AOSIS. This work is licensed under the Creative Commons Attribution License. The loss of large trees (> 5 m in height) in Africa's protected areas is often attributed to the impact by savanna elephants (Loxodonta africana). Concerns have been raised over large tree mortality levels in protected areas such as South Africa's Kruger National Park (KNP) and in the past, the need to manage its elephant population in order to preserve large trees and biodiversity as a whole. Our review aims to synthesise and discuss the complexities of managing elephants' effects on the landscape to ensure the survival of large trees, as well as the application purposes of the various lethal and non-lethal elephant mitigation strategies. We further critically evaluate past management strategies, which have solely focused on controlling elephant numbers to protect large trees. Past mitigation strategies focused on managing elephant impact by directly reducing elephant numbers. However, maintaining elephant numbers at a pre-determined carrying capacity level did not prevent the loss of large trees. Research on large tree survival in African savannas has continually exposed the complexity of the situation, as large tree survival is influenced at various demographic stages. In some cases, a coalescence of historical factors may have resulted in what could be perceived as an aesthetically appealing savanna for managers and tourists alike. Furthermore, the past high density of surface water within the KNP homogenised elephant impact on large trees by increasing the encounter rate between elephants and large trees. Our review evaluates how current mitigation strategies have shifted from purely managing elephant numbers to managing elephant distribution across impact gradients, thereby promoting heterogeneity within the system. Additionally, we discuss each mitigation strategy's occurrence at various landscape scales and its advantages and disadvantages when used to manage impact of elephant on large trees.

Conservation implications: A variety of options exist to manage the effects that elephants have on large trees. These options range from large-scale landscape manipulation solutions to small-scale individual tree protection methods. Interactions between elephants and large trees are complex, however, and conservation managers need to consider the advantages and disadvantages of each mitigation strategy to protect large trees.

Keywords: elephant impact; conceptual model; Kruger National Park; *Loxodonta africana*; mitigation strategies; spatial and temporal distribution.

Introduction

In South Africa, where savanna elephant (*Loxodonta africana*) populations and large trees have co-existed on fenced-off landscapes such as within the Kruger National Park (KNP), the impact of elephants on large trees is viewed by some as unsustainable (Asner et al. 2016; Edge et al. 2017). State officials and conservation managers are continuously involved in discussions concerned with managing the impacts of elephants in an attempt to protect large trees and maintain the natural system in an 'ideal' state, usually based on colonial historical records (Kerley et al. 2008) or driven by tourist perceptions or expectations of an aesthetic landscape (Edge et al. 2017). These records, however, coincide with the near-extermination of elephants in South Africa from over 100 000 individuals, as a consequence of recreational and subsistence hunting (Whyte 2001). Furthermore, an outbreak of rinderpest in the 19th century resulted in a herbivore population crash, decreasing the numbers of smaller browsers that would usually feed on tree seedlings (Skarpe et al. 2004).

In the post-culling era, elephant numbers have steadily increased (Ferreira, Greaver & Simms 2017), although their distribution ranges have decreased as a result of fencing off protected areas (Whyte 2001). South Africa is therefore dealing with the complexities of managing increasing elephant numbers in restricted ranges or landscapes with homogenous resource distribution, where an 'ideal' environmental state is the conservation goal to benefit tourism. The present

Read online:



Scan this QR code with your smart phone or mobile device to read online.



management strategy of the South African National Parks is focused on how elephants use their resources in relation to their distribution rather than absolute elephant numbers (Ferreira et al. 2017; SANParks 2012). The interplay between elephants and large trees is complex to the extent that no single species or factor can be thought of as solely responsible for what is essentially a multifaceted ecological process (Greyling 2004).

The aims of this review were to evaluate management methods to protect trees from elephant effects, in both small and large protected areas. We thereby firstly discuss the importance of large trees and how elephants interact with them, followed by a critical evaluation of the past management practices to reduce elephant numbers for protection of large trees. Lastly, we discuss the available management options to address the concern for the loss of large trees within a framework that highlights the various factors that potentially cause concern and the complexities of addressing a single mechanism within a heterogeneous landscape.

Why are large trees important?

Large trees (> 5 m in height) have a particular aesthetic significance to both the public and conservation managers (Shannon et al. 2008), being considered as important landscape features where they occur (Edge et al. 2017; Owen-Smith et al. 2006). The addition or reduction of large trees across a threshold is thus an indication of changing ecological states (Dublin, Sinclair & McGlade 1990). Importantly, a change in ecological state is not necessarily negative, as environments of a degraded nature may be recovering from past management practices (Young 2000).

Large trees have important ecosystem functions and play a significant role in the cycling of nutrients (Ludwig, De Kroon & Prins 2008), reduction of evapotranspiration and conductance for species which occur below the crowns of trees (Belsky 1994), as well as providing a forage source for fauna (Kerley & Landman 2006). Other than providing food and shelter, large trees provide nesting sites for both vultures and raptors (Vogel et al. 2014).

Elephant – large tree interactions

Elephants impact trees in a variety of means, ranging from bark-stripping and branch breakage, towards more destructive impacts such as uprooting and stem snapping (Greyling 2004). The type and intensity of elephant impacts are determined by a variety of factors, including tree species (Shannon et al. 2008), tree height (Cook et al. 2017) and elephant sexual dimorphism (Greyling 2004). Elephants have particular forage preferences for species, including the marula (*Sclerocarya birrea*), knobthorn (*Senegalia nigrescens*) and red bushwillow (*Combretum apiculatum*) trees (Shannon et al. 2008). Tree height can exacerbate elephant impact. For example, marula trees between 5 m and 11 m in height are more vulnerable to uprooting and stem snapping when

compared with trees above 11 m (Cook et al. 2017). Elephant bulls, being larger bodied, have heavier impacts on food species compared to cows (Greyling 2004).

More recent studies focused on the positive ecological/biodiversity consequences of elephant disturbance regimes (Guldemond, Purdon & Van Aarde 2017). The ability of elephants to modify and alter woody structure, however, can increase habitat complexity by modifying the woody structure (Sianga et al. 2017). The feeding habits of elephants can lead to 'hedging effects' on certain tree species (Lombard et al. 2001; Styles & Skinner 2000), which increase trees' vulnerability to both insect invasions and fire damage due to a reduction in tree height, volume or exposed inner tissues (Jacobs & Biggs 2002). The impact of elephants above a certain threshold can lead to loss of particular tree species within a landscape, as well as a decrease in the landscape's structural diversity (Asner et al. 2016; Eckhardt, Van Wilgen & Biggs 2000; McCleery et al. 2018).

Some studies have found that elephants can have a negative influence on biodiversity (Kerley & Landman 2006; McCleery et al. 2018) and woody canopy cover within protected areas (Asner et al. 2016). Extensive elephant feeding habits can displace black rhinoceros (Kerley & Landman 2014), which leads to increased predation of meso-herbivores owing to the opening of habitat (Tambling et al. 2013) and decreased foraging opportunities for micro-herbivores (Hrabar & Du Toit 2014). McCleery et al. (2018) have found that the combination of fires and elephant impact can lead to the removal of large trees in southern African savannas, decreasing the diversity of birds, bats and terrestrial small mammals.

Elephants play an important role in the propagation of large trees, in terms of both dispersal and germination of tree seeds. Mature bulls can transport seeds to a maximum distance of 65 km away from their source (Bunney, Bond & Henley 2017). Concurrently, the acid treatment in their digestive system promotes the germination of seeds (Cochrane 2003), while the deposition of seeds in parcels of organic mulch further promotes germination (Cochrane 2003). These processes are promoted by the inefficiency of elephants' digestive systems and their ability to produce 14–20 droppings per day with each defecation weighing around 11 kg, thereby enabling them to comfortably produce at least 150 kg of wet dung a day (Owen-Smith 1988).

Elephants also modify the landscape as ecosystem engineers, major tree pruners, effective composting agents and seed dispersers, thereby increasing biological diversity on a micro-scale (Valeix et al. 2011). Depending on the level of impact, this process has been found to increase the nutrient quality of impacted plants, escalate the overall biodiversity of the landscape and promote a mosaic of elephant impact-tolerant plant species closer to water points (Gaylard 2015; Kohi et al. 2011).

Hence, landscapes used by elephants will have altered vegetation structure, which leads to a higher diversity of ants, reptiles and frogs through the creation of micro-habitats (Nasseri, McBrayer & Schulte 2010; Palmer et al. 2008). The pruning activities of elephants can stimulate plant growth and also stimulate shoot production in height levels accessible for other browsers, thereby promoting foraging opportunities for other herbivores (Mograbi et al. 2017). Thus, further research is required on the management methods available for reducing elephant impact on the environment, and how biodiversity responds to changes in levels of elephant impact over time.

A critique of the justification used to reduce elephant numbers to save large trees

The precautionary principle

The precautionary principle, originated in Germany, describes the need to 'control inputs even before a causal link has been established by absolutely clear scientific evidence' (O'Riordan 2013), thereby applying a management action before damage is shown. Hence, there is no requirement to quantify damage before management action is applied (Milne 1993). This process therefore largely ignores rigorous scientific testing of certain hypotheses and outcomes, and base decisions on value judgements as opposed to adaptive management strategies (Rodgers 2005).

The precautionary principle has always been in favour of protecting large trees in the KNP, whether by means of culling elephants, manipulating elephant distributions through waterhole closures or directly protecting trees through mitigation methods (SANParks 2012). The safety margins provided by the precautionary principle favour a static environmental state within thresholds of potential concern, which may not always be applicable in a dynamic ecosystem (Maltby 2000).

Carrying capacity: A popular misconception

Between 1967 and 1994, elephant culling programmes in the KNP focused on maintaining the population at one elephant per square mile (0.4 elephants/km²) (Whyte 2001). The idea that the KNP can only maintain an elephant population of 7000 elephants has become entrenched in the minds of the general public, ignoring the concept that a carrying capacity of a static nature does not hold true in a complex ecological system (McLeod 1997). This entrenched mindset has brought about concerns of a potential overpopulation of elephants in the KNP, with the current elephant number at over 20 000 (Pretorius, Garaï & Bates 2018).

However, the revised elephant management plan (SANParks 2012) has shifted from focusing on elephant numbers as a whole, to maintaining ecological processes that uphold

ecosystems through manipulating the environment to create a gradient of elephant effects across the system (Ferreira et al. 2017; Guldemond et al. 2017). Elephants' spatio-temporal usage of the landscape differs in accordance to resource availability, influencing the distribution of elephant effects (Gaylard 2015). As elephants do not make use of the landscape uniformly, heterogeneity is promoted across areas of high and low elephant impact (Kerley et al. 2008). Management initiatives based on outdated agricultural concepts, for example carrying capacity, can no longer be implemented while a number of long-term studies have been initiated.

Fence-line contrasts

Exclosures and enclosures in an ecological system represent boundaries of continuums, allowing managers to evaluate which factors may influence the desired landscape they wish to achieve by comparing it with a similar landscape lacking the same drivers of change (Cowling & Kerley 2002). The northern KNP's 300-hectare roan antelope enclosure (N'waxitshumbe enclosure) has commonly been used for comparisons on how elephants and other herbivores have impacted the area's marula trees (Jacobs & Biggs 2002). What is evident is that large marula trees still disappeared from the landscape after many years of culling, even though the enclosure's fence was erected at the same time the KNP initiated elephant culling operations (Jacobs & Biggs 2002). Elephant culling only slowed the mortality rate of some large tree species, which illustrates how elephants have an impact on their preferred species regardless of their density (Owen-Smith 2005).

A lack of browsers in the roan enclosure supported the recruitment of marula seedlings into older age classes (Hofmeyr 2003), while browsers outside the enclosure such as impala (*Aepyceros melampus*) are known to heavily 'predate' large tree seedlings (Skarpe et al. 2004). Therefore, recruitment constraints of large trees can be attributed to herbivory at various age- and size-classes by a variety of ungulates, other than elephants (Helm & Witkowski 2012). Furthermore, carefully lit and controlled fires within the enclosure favoured young trees escaping the 'fire-trap', while other large trees in the enclosure have died as a result of natural attrition (Hofmeyr & Eckhardt 2005).

The absence of a direct relationship between the number of elephants and proportion of dead marula trees during the years of culling suggests that elephants are not solely responsible for the decline of marula trees, and that factors influencing the trees at various life history and demographic stages need to be considered within a broader ecological context (Kruger & Grant 2005). A growing body of evidence indicates that a complex nature exists between elephant impact (Asner et al. 2016), fire regimes (Smit et al. 2016) and climate change (Bond & Midgley 2012) on treefall rates and bush encroachment in southern African savannas.

Tsavo and Chobe National Parks: The importance of historical perspectives

Conflicting views exist over the temporary woodland loss in Tsavo National Park (TNP) owing to elephant impact (Chamaille-Jammes & Fritz 2005; Leuthold 1977; Parker 1983). Although the *Commiphora* woodlands were drastically decreased in the early 1970s (Leuthold 1977), significant recruitment and regeneration have occurred (Gillson 2004). Changes in species diversity within the TNP are largely undocumented (Owen-Smith 1988), as a decrease in browsing species during the temporary woodland loss was balanced by increased numbers of open grassland grazers (Parker 1983). Importantly, authorities are witnessing changes to landscapes where densities and sizes of established large trees may be representative of a time of low elephant numbers due to ivory poaching at the turn of the previous century.

Current, observed changes and fluctuations in vegetation types may be due to ecosystems returning to state where elephant numbers were more prevalent (Owen-Smith 1988). Furthermore, in the Chobe National Park (CNP), correlation does not necessarily imply causation, as is the case with elephant densities and changes to the vegetation's structural diversity. Species such as impala which have been recovering from the rinderpest outbreak in the late 1800s may be preventing the CNP's woodland regeneration and recruitment through high levels of seedling herbivory (Skarpe et al. 2004; Skarpe, Du Toit & Moe 2014).

According to population models, the CNP elephant population is increasing towards densities experienced prior to the 19th century ivory trade (Parker & Graham 1989). Likewise, vegetation structure and diversity may thus be reverting back to previous states under higher densities of elephants, making the prevention of this process an impractical management task (Robson et al. 2017). Vegetation impact by elephants in the CNP is localised, however, with scientific research failing to find overall concerns for a loss of biodiversity at a large scale (Owen-Smith 2005). Hence, no authentic reports have documented irreversible elephant impact by elephants on the CNP ecosystem (Owen-Smith 2005; Guldemond et al. 2017; Van Aarde et al. 2005).

Mitigation strategies amid the many factors potentially influencing the loss of large trees

In the past, the biodiversity objectives of the KNP were realised through the reduction in elephant numbers by culling operations (Whyte 2001). However, elephants represent only one facet of a multifaceted ecological process when it comes to survival rates of large trees (Figure 1). Elephant density alone does not explain demographics of large trees (Guldemond et al. 2017). This is in part due to many factors involved in the survival and recruitment rates of large trees (Helm, Scott & Witkowski 2011), as well as the spatial distribution of elephants (Sianga et al. 2017).

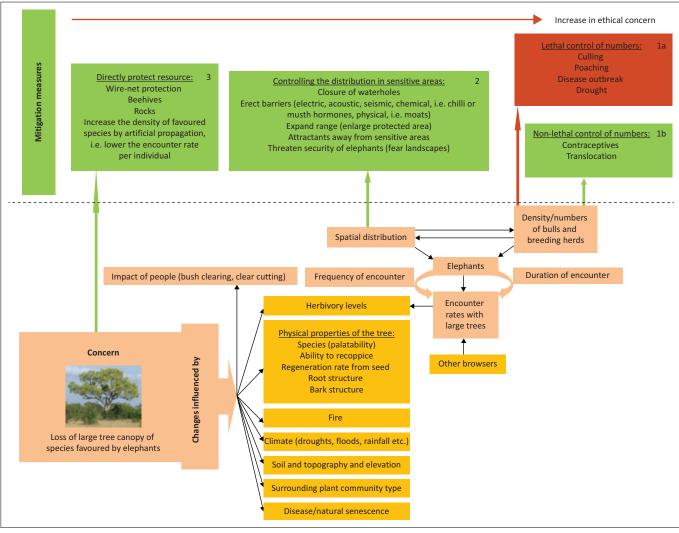
Elephant encounter rate and residence time with large trees are influenced by their density, as well as their spatial distribution (O'Connor, Goodman & Clegg 2007). The spatial distribution of elephants in turn depends on a variety of factors. These include both forage (Young, Ferreira & Van Aarde 2009) and water availability (De Knegt et al. 2011), rainfall (Birkett et al. 2012), the thermal environment (Kinahan, Pimm & Van Aarde 2007), fire (Woolley et al. 2008), roads when used as footpaths by elephants or because of increased forage productivity on their verges (Smit & Asner 2012), fences (Vanak, Thaker & Slotow 2010), terrain ruggedness (Wall, Douglas-Hamilton & Vollrath 2006) and the social and safety benefits of the areas they occupy (De Knegt et al. 2011).

Elephants, fire, soil and elevation have been found to be the main determinants of tree extirpation, but the rates of extirpation are also dependent on the plant species being affected (Asner et al. 2016; O'Connor et al. 2007). Species such as the mopane tree (*Colophospermum mopane*) are able to re-coppice post-elephant impact (Styles & Skinner 2000), while the weak coppicing abilities of knobthorn trees leave them more vulnerable to elephant impact (MacGregor & O'Connor 2004). Despite current increased atmospheric carbon dioxide levels, which promote the growth of woody vegetation, there is little bush encroachment where there are elephants and high-intensity fires (Stevens et al. 2016). Overall, large tree survival rates are thus influenced by the heterogeneity of the landscape in terms of elephant use and the interplay with differences in fire intensity.

Although elephant management interventions should not be considered in isolation from other drivers influencing large tree population dynamics, a number of options are still applicable if the management objective is to protect large trees. The mitigation strategies presented here focus on the ecological consequences without considering ethical concerns and can be divided into the following three types:

• Strategies aimed at directly affecting elephant numbers either (1) lethally or (2) by making use of non-lethal methods such as contraceptives or translocation (Figure 1: block 1a & 1b of mitigation measures, Table 1).

Lethal methods for population reduction: Past approaches have aimed at directly reducing elephant numbers with particular reference to culling and translocation. However, controlling an elephant population at an arbitrarily placed number prevents density-dependence feedbacks from playing a natural role in reducing the population's growth rate (Owen-Smith 2005; Robson & Van Aarde 2018). Culling of a population which is experiencing an exponential growth phase will habitually result in an increase in the birth rates of the population, as the availability of food per head is increased (Caughley 1983). Furthermore, interregional movements of elephants have been observed into areas where elephants have been previously culled, nullifying the intentional plan of protecting the vegetation through culling (Van Aarde et al. 2005). Definition of zones where



Source: Designed by author, Michelle D. Henley.

FIGURE 1: Conceptual model illustrating the aspects involved in addressing the concern for the loss of large trees of species favoured by elephants. Yellow boxes indicate factors unrelated to elephants, which are known to also affect large tree loss. Under mitigation strategies, the red box deals with factors that will directly affect elephant numbers and densities due to either removal of elephants or increased mortality rates. The green boxes highlight all available non-lethal mitigation strategies.

culling operations are meant to take place have also been found to mismatch the actual spatial and temporal movements of elephants (Delsink et al. 2013).

Elephant numbers can also be affected by poaching (Wittemyer et al. 2014), disease outbreak (Grobler et al. 1995) and drought (Loveridge et al. 2006), but these population control measures remain undesirable as they are often unexpected and notoriously difficult to manage. Poaching, in particular, has led to the demise of one-third of the African continental elephant population in the space of 7 years across primarily Central and East Africa (Chase et al. 2016; Wittemyer et al. 2014). Recently, poaching has also increased in the southern African states with the KNP experiencing the highest poaching incidents in decades (Lindsay et al. 2017).

Legal hunting has been suggested as a means to control elephant numbers; however, hunting is a highly selective activity, as bulls of particular age categories and with sought-after physical traits are targeted (Stalmans, Attwell & Estes 2002). For these reasons, hunting has not been listed as a population control method as it could result in undesirable skewed sex ratios and age structures within populations (Milner, Nilsen & Andreassen 2007).

Non-lethal methods for population reduction: Non-lethal methods used to control elephant numbers include the use of contraceptives (Delsink et al. 2007) and translocation (Grobler et al. 2008). The success of contraception as a management tool to control population numbers has been shown in a number of reserves in South Africa, including the Greater Makalali Private Game Reserve and Tembe Elephant Park (Bertschinger et al. 2018).

Translocation, however, is dependent on new available space for elephants, which is a limiting factor in South Africa (Grobler et al. 2008). Depending on the scale of the operation, translocation, as a means of reducing elephant numbers, may also have the same effect on elephant growth rates as culling had in the past (Caughley 1983). Both these non-lethal methods are currently of prime importance in smaller

TABLE 1: Advantages and disadvantages of elephant mitigation strategies to decrease elephant impact on large trees.

Man	nagement method		Advantages	Disadvantages	Literature
1a	Lethal control of numbers	Culling	Directly lowers elephant numbers in a specific area	Set 'carrying capacity' figures may not be ecologically sound	Greyling (2004)
			Products from carcasses can be sold as income for the protected area or distributed to neighbouring communities	Culling induces inter-regional movements and elephants breed at increased rates owing to increased availability of resources	Owen-Smith et al. (2006) Shannon et al. (2013)
				Bulls and cows exert different levels of impact on vegetation; so not only elephant numbers need consideration	Ferreira et al. (2017)
				 Expensive and logistically challenging to conduct on a large scale 	
				Social disruption to the population	
				 Ethical concerns are high and potential increase in aggression and/or stress in remaining population 	
				Potential tourism economic backlash	
		Poaching	May lower numbers to desirable management densities	Uncontrollable – cannot be managed by protected area	Wittemyer et al. (2014) Chase et al. (2016)
				Social disruption to population	
				 No economic benefit to protected area with tourism decreasing because of lowered photo tourism opportunities and potential safety hazards 	
		Disease	Natural form of mortalityMay be selective towards weaker individuals	Difficult to manage and requires high veterinary costs to control the spread of disease if threatening to all individuals	Grobler et al. (1995)
		Drought	Natural form of mortality Selective towards weaker individuals and juveniles	Periodic and uncontrollable	Loveridge et al. (2006)
				Public outcry especially where young animals are affected	
1b	Non-lethal control of numbers	Contraception	Reduction in population growth rateReversible	 Could be expensive to implement and maintain depending on the scale of implementation 	Van Aarde and Jackson (2007)
			Effective at containing population numbers at desirable densities in small enclosed protected areas, although populations with larger numbers of elephants are currently being placed on contraceptives	 May not be practical for controlling elephant numbers in large protected areas that don't want to resort to intense management strategies 	Delsink et al. (2007) Bertschinger et al. (2018)
				 Ethical concerns if young cows are not afforded allomothering processes 	
				 Behavioural studies of cows coming into oestrus four times a year instead of once every 4 years on average still under investigation and dependent on the type of contraceptive agent used 	
		Translocation	Directly reduces numbers and is a selective process	High costs for translocation equipment usage and veterinary fees	Millspaugh et al. (2007)
			Entire herds can be translocated to reduce individuals' stress levels	Lack of new protected areas to which elephants can be translocated	Grobler et al. (2008)
				 Elephants' stress levels increase during and after the translocating process 	
2	Controlling the distribution in sensitive areas	Closure of waterholes	Manipulates densities across the landscape in keeping with climatic cycles	Lag effect between the closure of waterholes and the desired effect on elephant densities	Smit et al. (2007)
			Creates a heterogeneous landscape, as certain areas closer to waterholes are utilised more than those further away	Requires large-scale implementation, which is not always possible in private protected areas	Purdon and Van Aarde (2017) Ferreira et al. (2017)
			Natural mortality amongst young and weak elephants during drought	Waterhole closures may negatively affect wildlife viewing for tourists	Robson and Van Aarde (2018)
			• Creates refugis locations for large	Coath to act we and resistant to be retired.	Sianga et al. (2017)
		Erect barriers	 Creates refugia locations for large trees by directly excluding elephants 	 Costly to set up and maintain barriers Elephants may still break through barriers to access excluded 	Western and Maitumo (2004)
			Ensures the protection of large trees' seed banks	resources	
				May not be aesthetically appealing	
		Expand range	 New areas become available to elephants, allowing populations to disperse over greater distances 	Human encroachment limits space availability for expansion of protected areas	Van Aarde and Jackson (2007)
			Potential to encourage seasonal migratory paths, decreasing density pressures within the original protected area	 Possible lag effect between the opening of new protected areas and the elephant movement into these areas 	Druce et al. (2008)
				Potential increase in human-elephant conflict with crops	
		Attractants away from sensitive areas	Most successful in conjunction with a water management plan	Difficult to implement in large protected areas, especially for protecting large trees	Rode et al. (2006)
			Salt blocks, for example, have been successfully used to manipulate elephant movements on a micro-scale	May not have the desired effect if water sources are still available in the desired area	
		Landscape of fear	Possibility of exposed elephants passing on knowledge of the 'landscape of fear' to other	Need to ensure unpredictability of environment or else elephants become habituated	Douglas-Hamilton et al. (2005)
			'Landscape of fear' areas, which discourage high elephant densities, promote heterogeneity across the landscape	Ethical concerns are high depending on the methods used to create a 'landscape of fear'	Cromsigt et al. (2013)
				Potential tourism economic backlash	

Table 1 continues on the next page \rightarrow

TABLE 1 (Continues...): Advantages and disadvantages of elephant mitigation strategies to decrease elephant impact on large trees.

Ma	nagement method		Advantages Effective at protecting individual trees from bark-stripping	Disadvantages Does not protect trees from heavier elephant impacts (e.g. stem snapping and uprooting)	Derham et al. (2016) Cook et al. (2018)
3	Directly protect resource	Wire-net protection			
			Inexpensive to set up and little maintenance required	Wire-net may be ripped off by elephants if not maintained or securely applied	
		Beehives	Effective at protecting individual trees from elephant impact	Expensive to set up and maintain	Cook et al. (2018)
				Sensitive to drought conditions	
			Honey from beehives can be harvested for additional income	Overloading environment with honeybees may exclude other pollinators	
			 Pollination services from honeybees 		
		Rocks	Inexpensive to set up and little maintenance required	Large quantities of rocks are needed to keep elephants away	SANParks (2012)
			May be more aesthetically appealing versus wire-netting and beehives	Rocks can be kicked away or stepped over by elephants if not maintained	
				 Not practical in areas lacking natural rocky terrain 	
				Initial disturbance of cryptic micro-fauna and insects	
		Artificial propagation of	 Increases the density of large trees in a refugia location 	Does not target the loss of large trees within the protected area and should therefore be used in conjunction with other	Hofmeyr and Eckhard (2005)
		favoured species	 Inexpensive to carry out once a suitable location is identified 	management plans	Scholtz 2007
			Ensures the protection of large trees' seed banks	Difficult and costly to protect seedlings against all herbivores	

Note: Coding in the first column is in alignment with the coding categories from Figure 1.

reserves with limited options for expansion or dispersal of animals and high tourism investment.

• Strategies aimed at manipulating the environment to influence the spatial distribution of elephants (Figure 1: block 2 of mitigation measures, Table 1).

Overall, elephant impact is regulated by resource abundance and thereby, this impact can be spatially and temporarily altered by modifying how accessible resources are to elephants, thus promoting heterogeneity (Sianga et al. 2017). Modified elephant impact, both spatially and temporally, leads to greater levels of biodiversity on a regional scale (Gaylard 2005; Sianga et al. 2017).

Surface water availability is an important driving factor behind elephant distributions (Gaylard, Owen-Smith & Redfern 2003). A scarcity of water can result in refugia localities for particular plant species (Eckhardt et al. 2000), as elephant movement ranges are naturally heterogeneous in accordance with surface water distribution (Gaylard et al. 2003). Elephant impact is thus homogenised in areas containing a high density of water points, as movement ranges are spatially and temporally reduced (Gaylard 2015). Smit, Grant and Whyte (2007) found that bulls in the KNP are more likely to occur further from natural rivers in comparison to breeding herds, making use of the availability of artificial waterholes to expand their spatial range. The KNP has used the closure and spatial distribution of artificial waterholes to manipulate elephant movement ranges, as well as their impact on vegetation (Ferreira et al. 2017; Macfadyen et al. 2019; O'Connor et al. 2007; Shannon et al. 2008). Intense levels of impact occur around the surface water points, while impact decreases as distance to surface water increases (Gaylard 2005). Sianga et al. (2017) found that large tree populations were abundant > 10 km from surface water in the Okavango Delta and Linyanti Swamps. Furthermore, the eventual scarcity of resources around a limited supply of water could lead to a situation where an elephant population that is double its size but increasing at half its rate would result in the same surplus of individuals (Owen-Smith 2005; Robson & Van Aarde 2018).

Waterhole closure in the KNP has already reduced the annual population growth rate from 6.5% to 4.2% over a 12-year period (Ferreira et al. 2017). It has, however, been suggested that a lag phase may occur between the closure of waterholes and a reduction in elephant impact on trees in the KNP (SANParks 2012). Furthermore, this method may not be viable in small protected areas where it is not spatially realistic to create gradients of elephant impact. Importantly though, reducing waterholes can also reduce the residency of water-dependent browsers of seedlings, such as impala (Skarpe et al. 2004). Reducing environmental pressures on the seedlings of large trees will aid in the recruitment of mature individuals.

Other methods used to manipulate elephants' distribution include the use of barriers or hard boundaries. Fences are the most commonly used barriers, but a variety of other barrier types can also be implemented (SANParks 2012).

In open systems, elephants can adapt their behaviour when exposed to temporal and spatial variability of resources (Owen-Smith 2005). The colonisation of new areas by less risk-adverse bulls (Whyte 2001) could be of great value in alleviating impact on vegetation within current home ranges, as bulls exert greater levels of impact on the vegetation in comparison to cows and calves (Greyling 2004). This dispersal can be temporally delayed, as Druce et al. (2008) found that older elephant bulls in South Africa's Phinda Private Game Reserve took 1 month to move into two neighbouring reserves following the dropping of fences, while younger bulls and breeding herds took 5 to 8 months to follow. Dispersal of elephants can be a result of increased densities of

elephants and this process could be disrupted by pre-emptive culling, which does not allow source areas to reach the required densities, which would encourage dispersal. Dispersal movements can be further encouraged by ensuring that important movement corridors, identified through the movements of collared individuals, are kept open and protected (Douglas-Hamilton, Krink & Vollrath 2005).

Elephants may also avoid areas if deemed unsafe. Fear landscapes can influence elephant distribution patterns as elephants avoid areas where threats to their safety are perceived as spatially predictable, but the timing and type of threat remains unpredictable (Cromsigt et al. 2013). Indeed, the density of elephants immediately decreased in zones where culling had commenced in KNP, before elephants immigrated back to these zones within the following years (Van Aarde, Whyte & Pimm 1999). Conversely, safety benefits can thus be used as one method to attract elephants to particular areas. Hence, environmental manipulation could be applied and monitored in an adaptive management approach to encourage elephants into particular areas where their population growth rates would be limited by natural processes (Robson & Van Aarde 2018).

• Strategies aimed at directly protecting the resource, for example large trees (Figure 1: block 3 of mitigation measures, Table 1).

Tree sanctuaries can be formed from the direct protection of the resource (i.e. large trees). In addition to preserving the aesthetic importance of landscape features such as large trees, mature specimens could serve as important seed banks for future recruitment programmes (Western & Maitumo 2004).

Wire-netting tree trunks have been found to increase the survival rate of large trees as the technique essentially prevents bark-stripping by elephants. However, treated trees do remain susceptible to branch breakage, uprooting or main stem snapping, albeit at lower frequencies (Derham, Henley & Schulte 2016).

The use of African honeybees (*Apis mellifera* subsp. *scutellata*) has proved to be a highly effective, albeit costly, mitigation method for protecting individual trees from elephant impact (Cook et al. 2018). Potentially, the costs can be offset by the production of honey and the additional pollination services obtained from active beehives.

Other methods used to protect large trees involve the packing of rocks and pyramids around the base of a tree to a distance of up to 5 m from the stem (SANParks 2012). The efficacy of this technique has not been quantified in the scientific literature, although anecdotal evidence indicates that it could be effective if laid out correctly.

Importantly, methods that directly protect the individual tree will have a small spatial effect, but no lag time with regard to their effectiveness. These methods are applicable in both small and large protected areas where individual trees are in need of protection.

Lastly, the artificial propagation of seedlings of woody species favoured by elephants in exclusion experiments can be viewed as another method to increase the density of food plants while reducing encounter rates with elephants (Hofmeyr 2005). This method, while not yet tried in South Africa, provides an alternative option to lowering elephant densities to achieve the same effect. Experimental exclosures in the Mapungubwe National Park have demonstrated the potential of artificial propagation as a means of assisting big tree regeneration (Scholtz 2007). Artificial propagation has further been used to help diminish human–elephant conflict in Thailand (Van de Water & Matteson 2018).

Elephant meta-population management

Each of the proposed mitigation strategies have certain advantages and disadvantages associated with them (Table 1), many of which also need to be evaluated from an ethics perspective (broadly listed from most severe to least severe ethical concern in Figure 1 and Table 1), as increased interference and disruption of intact social systems can occur when moving from strategy three to strategy one. However, elephants are continually exposed to a wide range of stresses across the landscape, and their response to such stressors can be used to evaluate the ethics and effectiveness of proposed mitigation strategies. Understanding how elephants respond to human-induced fear (Douglas-Hamilton et al. 2005) and resource manipulation (Purdon & Van Aarde 2017) will be important when mitigation strategies are implemented.

In the Great Limpopo Transfrontier Park (GLTP, 37 572 km²), all three abovementioned mitigation strategies are being carried out across the system. The density of elephant poaching is the highest in the Limpopo National Park (Lunstrum 2014), which would affect elephant densities and create sink areas driven by fear (Van Aarde & Jackson 2007). These landscapes of fear influence both the density and spatial distribution of elephants concurrently, albeit undesirably because poaching is known to disrupt the social structure and demographics of the population and is hard to control (Jones et al. 2018). Future research is required to evaluate the effect that poaching in the Limpopo National Park and the slow increase within the KNP will have on the higher elephant population density and vegetation composition found within the KNP and neighbouring reserves. Key to elephant management within the KNP would be to increase the safety benefits within the neighbouring Limpopo National Park to which elephants will naturally respond in keeping with seasons and as this reserve only has a seasonal and natural spread of available surface water.

Historically, the KNP reduced elephant numbers through culling and although these practices are no longer implemented partly because they were unsuccessful in achieving the desired outcome – for example the protection of large trees –

the KNP is experiencing some of the highest poaching records in its history (Lindsay et al. 2017). However, as the KNP still has an expanding elephant population (Ferreira et al. 2017), management is preferentially focusing on the second mitigation strategy by primarily controlling elephant distribution through artificial waterhole closure and have already closed two-thirds of the 365 artificial waterholes and 50 earth dams since it began its water stabilisation programme in the early 1930s (Purdon & Van Aarde 2017; SANParks 2012).

The Associated Private Nature Reserves (APNR) to the west of the KNP have a saturated water landscape and also a high density of landowners and lodges (Peel 2009). The landscape use implemented in this self-funded protected area may thus not lend itself to the aforementioned mitigation strategies. The APNR have, however, successfully implemented various mitigation strategies aimed at directly protecting the resource (large trees) such as wire-netting (Derham et al. 2016), African honeybees (Cook et al. 2018) and rocks and pyramids (Henley & Cook 2018). In smaller reserves (< 1000 km²), elephant range size is often a function of the size of the reserve (Roux 2006).

The manipulation or closure of waterholes may have a limited effect on reducing elephant impact on large trees in the APNR due to the immense number of waterholes distributed across private properties. As previously discussed, translocation may be a temporary option, although limited by the number of reserves that can support elephant populations (Grobler et al. 2008). Smaller reserves should focus on methods that directly protect large trees from elephant impact (Table 1) and investigate the potential of contraception for managing their elephant numbers (Table 1).

Botanical reserves that exclude elephants from particular floral communities within smaller reserves can also ensure the survival of large tree species and their seed banks (Lombard et al. 2001). Efforts should also be focused on large tree regeneration and recruitment, by considering factors such as seed predation (Helm et al. 2011), seedling herbivory (Skarpe et al. 2004) and fires (Smit et al. 2016), which are known to affect large tree survival, even in the absence of elephants (Helm & Witkowski 2012).

Conclusion

Conservation managers are faced with the difficulties of fulfilling their mandate of protecting biodiversity in humandominated landscapes and what biodiversity should be protected where objectives may be in conflict. Can large trees and elephants coexist and what strategies should managers implement to optimise biodiversity goals? These strategies should reflect on (1) implementing limited or no interventions when ecological processes are playing out (Biggs et al. 2008), (2) restoring ecological processes and opportunities if the landscape is termed 'degraded' (Wassenaar, Ferreira & Van Aarde 2007), and (3) mimicking desired ecological

processes if restoration is not possible (SANParks 2012). Hence, an adaptive management plan needs to consider and continually evaluate whether the proposed mitigation strategy will lead to the desired effect with:

- the least amount of interference to operating ecological processes both within the proposed area where the management action is to be applied, as well as in the surrounding landscape
- the least financial expenditure in terms of implementation for sustainability of the mitigation strategy
- the most practically implementable methods for both short-term and long-term tree survival
- the most ethical approach, in terms of either pain/trauma caused to individual elephants themselves or the disruption of their social relationships, in keeping with the Norms and Standards for Managing Elephants in South Africa (DEAT 2008). This is particularly true in areas dependent on tourism as socially disrupted populations could increase safety risks for tourists.

The three possible mitigation strategies available to potentially protect large trees can each be evaluated given the size of the reserve and historical perspectives. Protected areas such as the KNP, which forms part of a large open system, have opted for environmental manipulation as the management strategy. Although environmental manipulation may be viable for a reserve of this size, it may not prove appropriate in smaller protected areas. Here, a combination of directly protecting the resource (large trees) from elephant impact, in combination with translocations or contraceptive programmes, may prove more appropriate.

Acknowledgements

We would like to acknowledge various scientists who through the years have helped to shape these thoughts. In particular: Prof. Norman Owen-Smith, Prof. Johan du Toit, Prof. William Bond, Prof. Hennie Lotter and Dr Sam Ferreira.

Competing interests

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

Authors' contributions

M.D.H. was responsible for conceptualising the manuscript, writing the text and creating the conceptual model. R.M.C. was responsible for literature reviews and contributing towards the manuscript's text. Both authors reviewed drafts and approved the final draft of the manuscript.

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Funding information

Funding was received from the United States Fish and Wildlife Service, the Oak Foundation and many other smaller funders and private donors.

Data availability statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of any affiliated agency of the authors.

References

- Asner, G.P., Vaughn, N., Smit, I.P. & Levick, S., 2016, 'Ecosystem-scale effects of megafauna in African savannas', *Ecography* 39(2), 240–252. https://doi.org/10.1111/ecog.01640
- Belsky, A.J., 1994, 'Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition', *Ecology* 75(4), 922–932. https://doi.org/ 10.2307/1939416
- Bertschinger, H.J., Delsink, A., Van Altena, J.J. & Kirkpatrick, J.F., 2018, 'Porcine zona pellucida vaccine immunocontraception of African elephant (Loxodonta africana) cows: A review of 22 years of research', Bothalia African Biodiversity & Conservation 48(2), 1–8. https://doi.org/10.4102/abc.v48i2.2324
- Biggs, H.C., Slotow, R., Scholes, B., Carruthers, J., Van Aarde, R., Kerley, G. et al., 2008, 'Towards integrated decision-making for elephant management', in R.J. Scholes & K.G. Mennell (eds.), Assessment of South African elephant management, pp. 537–586, Witwatersrand University Press, Johannesburg.
- Birkett, P.J., Vanak, A.T., Muggeo, V.M., Ferreira, S.M. & Slotow, R., 2012, 'Animal perception of seasonal thresholds: Changes in elephant movement in relation to rainfall patterns', *PLoS One* 7(6), e38363. https://doi.org/10.1371/journal.pone.0003546
- Bond, W.J. & Midgley, G.F., 2012, 'Carbon dioxide and the uneasy interactions of trees and savannah grasses', *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1588), 601–612. https://doi.org/10.1098/rstb.2011.0182
- Bunney, K., Bond, W.J. & Henley, M., 2017, 'Seed dispersal kernel of the largest surviving megaherbivore The African savanna elephant', *Biotropica* 49(3), 395–401. https://doi.org/10.1111/btp.12423
- Caughley, G., 1983, 'Dynamics of large mammals and their relevance to culling', in R.N. Owen-Smith (ed.), Management of large mammals in African conservation areas, Proceedings of a Symposium Pretoria, South Africa, April 1982. Pretoria: Cooperative Scientific Programmes, Council for Scientific and Industrial Research, Pretoria
- Chamaille-Jammes, S. & Fritz, H., 2005, 'Rainfall drivers of dry season savanna productivity', in C.C. Grant (ed.), *Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks*, p. 22, Scientific Services, Skukuza, Scientific Report 3/2005.
- Chase, M.J., Schlossberg, S., Griffin, C.R., Bouché, P.J., Djene, S.W., Elkan, P.W. et al., 2016, 'Continent-wide survey reveals massive decline in African savannah elephants', *Peer Journal 4*, e2354. https://doi.org/10.7717/peerj.2354
- Cochrane, E.P., 2003, 'The need to be eaten: *Balanites wilsoniana* with and without elephant seed-dispersal', *Journal of Tropical Ecology* 19(5), 579–589. https://doi.org/10.1017/S0266467403003638
- Cook, R.M., Parrini, F., King, L.E., Witkowski, E.T.F. & Henley, M.D., 2018, 'African honeybees as a mitigation method for elephant impact on trees', *Biological Conservation* 217, 329–336. https://doi.org/10.1016/j.biocon.2017.11.024
- Cook, R.M., Witkowski, E.T.F., Helm, C.V., Henley, M.D. & Parrini, F., 2017, 'Recent exposure to African elephants after a century of exclusion: Rapid accumulation of marula tree impact and mortality, and poor regeneration', Forest Ecology and Management 401, 107–116. https://doi.org/10.1016/j.foreco.2017.07.006
- Cowling, R. & Kerley, G.I.H., 2002, 'Impacts of elephants on the flora and vegetation of subtropical thicket in the Eastern Cape', in *Elephant conservation and management in the Eastern Cape: Workshop Proceedings*, pp. 55–72, Terrestrial Ecology Research Unit, University of Port Elizabeth, Port Elizabeth, South Africa, Report (No. 35).
- Cromsigt, J.P., Kuijper, D.P., Adam, M., Beschta, R.L., Churski, M., Eycott, A. et al., 2013, 'Hunting for fear: Innovating management of human–wildlife conflicts', *Journal of Applied Ecology* 50(3), 544–549. https://doi.org/10.1111/1365-2664.12076
- DEAT, 2008, 'National environmental management: Biodiversity act, 2004 (act no. 10 of 2004) national norms and standards for the management of elephants in South Africa', Staatskoerant 30833(251), 3–39.

- De Knegt, H.J., Van Langevelde, F., Skidmore, A.K., Delsink, A., Slotow, R., Henley, S. et al., 2011, 'The spatial scaling of habitat selection by African elephants', *Journal of Animal Ecology* 80(1), 270–281. https://doi.org/10.1111/j.1365-2656.2010.01764.x
- Delsink, A.K., Van Altena, J.J., Grobler, D., Bertschinger, H.J., Kirkpatrick, J.F. & Slotow, R., 2007, 'Implementing immunocontraception in free-ranging African elephants at Makalali Conservancy', *Journal of the South African Veterinary Association* 78(1), 25–30. http://hdl.handle.net/10520/EJC99704
- Delsink, A., Vanak, A.T., Ferreira, S. & Slotow, R., 2013, 'Biologically relevant scales in large mammal management policies', *Biological Conservation* 167(2013), 116–126. https://doi.org/10.1016/j.biocon.2013.07.035
- Derham, K., Henley, M.D. & Schulte, B.A., 2016, 'Wire netting reduces African elephant (*Loxodonta africana*) impact to selected trees in South Africa', *Koedoe* 58(1), 1–7. https://doi.org/10.4102/koedoe.v58i1.1327
- Douglas-Hamilton, I., Krink, T. & Vollrath, F., 2005, 'Movements and corridors of African elephants in relation to protected areas', *Naturwissenschaften* 92(4), 158–163. https://doi.org/10.1007/s00114-004-0606-9
- Druce, D.J., Shannon, G., Page, B.R., Grant, R. & Slotow, R., 2008, 'Ecological thresholds in the savanna landscape: Developing a protocol for monitoring the change in composition and utilisation of large trees', PLoS One 3(12), e3979. https://doi.org/ 10.1371/journal.pone.0003979
- Dublin, H.T., Sinclair, A.R. & McGlade, J., 1990, 'Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands', *The Journal of Animal Ecology* 59(3), 1147–1164. https://doi.org/10.2307/5037
- Eckhardt, H.C., Van Wilgen, B.W. & Biggs, H.C., 2000, 'Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998', African Journal of Ecology 38(2), 108–115. https://doi.org/10.1046/j.1365-2028. 2000.00217.x
- Edge, A., Henley, M., Daday, J. & Schulte, B.A., 2017, 'Examining human perception of elephants and large trees for insights into conservation of an African savanna ecosystem', *Human Dimensions of Wildlife* 22(3), 231–245. https://doi.org/10.10 80/10871209.2017.1298168
- Ferreira, S.M., Greaver, C. & Simms, C., 2017, 'Elephant population growth in Kruger National Park, South Africa, under a landscape management approach', *Koedoe* 59(1), 1–6. https://doi.or/10.4102/koedoe.v59i1.1427
- Gaylard, A., 2015, 'Adopting a heterogeneity paradigm for understanding and managing elephants for biodiversity: A case study in riparian woodlands in Kruger National Park', PhD thesis, Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa, viewed 20 May 2018, from http://hdl.handle. net/10539/19327.
- Gaylard, A., Owen-Smith, R.N. & Redfern, J., 2003, 'Surface water availability: Implications for heterogeneity and ecosystem processes', in R.J. Scholes & K.G. Mendell (eds.), Elephant management: A scientific assessment for South Africa, pp. 171–188, Witwatersrand University Press, Johannesburg.
- Gillson, L., 2004, 'Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya', Ecological Complexity 1(4), 281–298. https://doi.org/10.1016/j.ecocom.2004.06.001
- Greyling, M.D., 2004, 'Sex and age related distinctions in the feeding ecology of the African elephant, Loxodonta africana', PhD thesis, Faculty of Science, University of the Witwatersrand, Johannesburg, viewed 14 April 2018, from http://hdl.handle. net/10539/7489.
- Grobler, D.G., Raath, J.P., Keet, D.F., Gerdes, G.H., Barnard, B.J.H., Kriek, N.P.J. et al., 1995, 'An outbreak of encephalomyocarditis-virus infection in free-ranging African elephants in the Kruger National Park', Onderstepoort Journal of Veterinary Research 62(2), 97–108.
- Grobler, D.G., Van Altena, J.J., Malan, J.H. & Mackey, R.L., 2008, 'Elephant translocation', in R.J. Scholes & K.G. Mendell (eds.), Elephant management: A scientific assessment for South Africa, pp. 241–256, Witwatersrand University Press, Johannesburg.
- Guldemond, R.A., Purdon, A. & Van Aarde, R.J., 2017, 'A systematic review of elephant impact across Africa', PLoS One 12(6), e0178935. https://doi.org/10.1371/journal. pone.0178935
- Helm, C.V., Scott, S.L. & Witkowski, E.T.F., 2011, 'Reproductive potential and seed fate of Sclerocarya birrea subsp. caffra (marula) in the low altitude savannas of South Africa', South African Journal of Botany 77(3), 650–664. https://doi.org/10.1016/j. sajb.2011.02.003
- Helm, C.V. & Witkowski, E.T.F., 2012, 'Characterising wide spatial variation in population size structure of a keystone African savanna tree', Forest Ecology and Management 263, 175–188. https://doi.org/10.1016/j.foreco.2011.09.024
- Henley, M.D. & Cook, R.M., 2018, *Elephants & big trees: Mitigation methods*, Unpublished report to the Associated Private Nature Reserves, 25 p.
- Hofmeyr, M., 2003, The spatial demography of elephant impacts on selected tree species in the Kruger National Park, Unpublished report to the US Fish and Wildlife, Skukuza, 43 p.
- Hofmeyr, M., 2005, 'Spatial demography of selected tree species in the Kruger National Park in relation to elephant impacts', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 61–67, Scientific Services, Skukuza, Scientific Report 3/2005.
- Hofmeyr, M. & Eckhardt, H., 2005, 'Changes in vegetation in the KNP related to elephant activity', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 50–57, Scientific Services, Skukuza. Scientific Report 3/2005.

- Hrabar, H. & Du Toit, J.T., 2014, 'Interactions between megaherbivores and microherbivores: Elephant browsing reduces host plant quality for caterpillars', *Ecosphere* 5(1), 1–6. https://doi.org/10.1890/ES13-00173.1
- Jacobs, O.S. & Biggs, R., 2002, 'The status and population structure of the marula in the Kruger National Park', South African Journal of Wildlife Research 32(1), 1–12. https://doi.org/10520/EJC117144
- Jones, T., Cusack, J.J., Pozo, R.A., Smit, J., Mkuburo, L., Baran, P. et al., 2018, 'Age structure as an indicator of poaching pressure: Insights from rapid assessments of elephant populations across space and time', Ecological Indicators 88, 115–125. https://doi.org/10.1016/j.ecolind.2018.01.030
- Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., De Boer, W.F. et al., 2008, 'Effects of elephant on ecosystems and biodiversity', in R.J. Scholes & K.G. Mendell (eds.), Elephant management: A scientific assessment for South Africa, pp. 146–205, Witwatersrand University Press, Johannesburg.
- Kerley, G.I.H. & Landman, M., 2006, 'The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets', South African Journal of Science 102(9–10), 395–402, viewed 20 May 2018, from http://hdl.handle.net/10520/EJC96608
- Kinahan, A.A., Pimm, S.L. & Van Aarde, R.J., 2007, 'Ambient temperature as a determinant of landscape use in the savanna elephant', Loxodonta africana. Journal of Thermal Biology 32(1), 47–58. https://doi.org/10.1016/j.jtherbio.2006.09.002
- Kohi, E.M., De Boer, W.F., Peel, M.J., Slotow, R., Van der Waal, C., Heitkönig, I.M., Skidmore, A. & Prins, H.H., 2011, 'African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna', *Biotropica* 43(6),711–721. https://doi.org/10.1111/j.1744-7429.2010.00724.x
- Kruger, L. & Grant, R., 2005, 'Chapter summary and conclusion', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 194–202, Scientific Services, Skukuza, Scientific Report 3/2005
- Leuthold, W., 1977, 'Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya', *Zeitschrift fur Saugetierkunde* 42(6), 358–379.
- Lindsay, K., Chase, M., Landen, K. & Nowak, K., 2017, 'The shared nature of Africa's elephants', *Biological Conservation* 215, 260–267. https://doi.org/10.1016/j.biocon.2017.08.021
- Lombard, A.T., Johnson, C.F., Cowling, R.M. & Pressey, R.L., 2001, 'Protecting plants from elephants: Botanical reserve scenarios within the Addo Elephant National Park, South Africa', Biological Conservation 102(2), 191–203. https://doi.org/10.1016/S0006-3207(01)00056-8
- Loveridge, A.J., Hunt, J.E., Murindagomo, F. & Macdonald, D.W., 2006, 'Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah', *Journal of Zoology* 270(3), 523–530. https://doi.org/10.1111/j.1469-7998.2006.00181.x
- Ludwig, F., De Kroon, H. & Prins, H.H., 2008, 'Impacts of savanna trees on forage quality for a large African herbivore', *Oecologia* 155(3), 487–496. https://doi.org/10.1007/s00442-007-0878-9
- Lunstrum, E., 2014, 'Green militarization: Anti-poaching efforts and the spatial contours of Kruger National Park', *Annals of the Association of American Geographers* 104(4), 816–832. https://doi.org/10.1080/00045608.2014.912545
- MacFadyen, S., Hui, C., Verburg, P.H. & Teeffelen, A.J.A., 2019, 'Spatiotemporal distribution dynamics of elephants in response to density, rainfall, rivers and fire in Kruger National Park, South Africa', Diveristy and Distributions 25(6), 880-894. https://doi.org/10.1111/ddi.12907
- MacGregor, S.D. & O'Connor, T.G., 2004, 'Response of Acacia tortilis to utilization by elephants in a semi-arid African savanna', South African Journal of Wildlife Research 34(1), 55–66, viewed 13 May 2018, from http://hdl.handle.net/10520/EJC117183.
- Maltby, E., 2000, 'Ecosystem approach: From principle to practice', Ecosystem Service and Sustainable Watershed Management in North China International Conference, China, 23rd–25th August, pp. 23–25.
- McCleery, R., Monadjem, A., Baiser, B., Fletcher, Jr., R., Vickers, K. & Kruger, L., 2018, 'Animal diversity declines with broad-scale homogenization of canopy cover in African savannas', *Biological Conservation* 226(2018), 54–62. https://doi.org/10.1016/j.biocon.2018.07.020
- McLeod, S.R., 1997, 'Is the concept of carrying capacity useful in variable environments?', Oikos 79, 529–542. https://doi.org/10.2307/3546897
- Millspaugh, J.J., Burke, T., Van Dyk, G.U.S., Slotow, R.O.B., Washburn, B.E. & Woods, R.J., 2007, 'Stress response of working African elephants to transportation and safari adventures', *The Journal of Wildlife Management* 71(4), 1257–1260. https://doi.org/10.2193/2006-015
- Milne, A., 1993, 'The perils of green pessimism', New Scientist 138(1877), 34–37.
- Milner, J.M., Nilsen, E.B. & Andreassen, H.P., 2007, 'Demographic side effects of selective hunting in ungulates and carnivores', *Conservation Biology* 21(1), 36–47. https://doi.org/10.1111/j.1523-1739.2006.00591.x
- Mograbi, P.J., Asner, G.P., Witkowski, E.T., Erasmus, B.F., Wessels, K.J., Mathieu, R. et al., 2017, 'Humans and elephants as treefall drivers in African savannas', Ecography 40(11), 1274–1284. https://doi.org/10.1111/ecog.02549
- Nasseri, N.A., McBrayer, L.D. & Schulte, B.A., 2011, 'The impact of tree modification by African elephant (Loxodonta africana) on herpetofaunal species richness in northern Tanzania', *African Journal of Ecology* 49(2), 133–140. https://doi.org/10.1111/j.1365-2028.2010.01238.x
- O'Connor, T.G., Goodman, P.S. & Clegg, B., 2007, 'A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa', *Biological Conservation* 136(3), 329–345. https://doi.org/10.1016/j.biocon.2006.12.014
- O'Riordan, T., 2013, Interpreting the precautionary principle, Routledge, Abingdon,

- Owen-Smith, R.N., 1988, Megaherbivores The influence of very large body size on ecology, Cambridge University Press, Cambridge.
- Owen-Smith, R.N., 2005, 'Ecosystem resources influencing elephant populations', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 41–42, Scientific Services, Skukuza, Scientific Report 3/2005.
- Owen-Smith, N., Slotow, R., Kerley, G.I.H., Van Aarde, R.J. & Page, B., 2006, 'A scientific perspective on the management of elephants in the Kruger National Park and elsewhere: Elephant conservation', South African Journal of Science 102(9), 389–394
- Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M. & Karban, R., 2008, 'Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna', Science 319(5860), 192–195. https://doi/10.1126/science. 1151579
- Parker, I.S.C., 1983, 'The Tsavo story: An ecological case history', in R.N. Owen-Smith (ed.), Management of large mammals in African conservation areas, pp. 37–49, Haum, Pretoria.
- Parker, I.S.C. & Graham, A.D., 1989, 'Elephant decline (Part I) downward trends in African elephant distribution and numbers', *International Journal of Environmental Studies* 34(4), 287–305. https://doi.org/10.1080/00207238908710539
- Peel, M., 2009, Management plan: Associated private nature reserves, Unpublished land owner document, 271 p.
- Pretorius, Y., Garaï, M.E. & Bates, L.A., 2018, 'The status of African elephant Loxodonta africana populations in South Africa', *Oryx* 1–7. https://doi.org/10.1017/S003060 5317001454
- Purdon, A. & Van Aarde, R.J., 2017, 'Water provisioning in Kruger National Park alters elephant spatial utilisation patterns', *Journal of Arid Environments* 141, 45–51. https://doi.org/10.1016/j.jaridenv.2017.01.014
- Robson, A.S., Trimble, M.J., Purdon, A., Young-Overton, K.D., Pimm, S.L. & Van Aarde, R.J., 2017, 'Savanna elephant numbers are only a quarter of their expected values', *PLoS One* 12(4), e0175942. https://doi.org/10.1371/journal.pone.0175942
- Robson, A.S. & Van Aarde, R.J., 2018, 'Changes in elephant conservation management promote density-dependent habitat selection in the Kruger National Park', *Animal Conservation* 21(4), 302–312. https://doi.org/10.1016/j.jaridenv.2017. 01.014
- Rode, K.D., Chiyo, P.I., Chapman, C.A. & McDowell, L.R., 2006, 'Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour', *Journal of Tropical Ecology* 22(4), 441–449. https://doi.org/10.1017/ S0266467406003233
- Rodgers, K.H., 2005, 'Elephant and biodiversity A synthesis of current understanding of the role and management of elephant in savanna ecosystems. Outcomes of the Science workshop, Luiperdskloof', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 227–234, Scientific Services, Skukuza. Scientific Report 3/2005.
- Roux, C., 2006, 'Feeding ecology, space use and habitat selection of elephants in two enclosed game reserves in the Eastern Cape Province, South Africa', Doctoral dissertation, Rhodes University.
- SANParks, 2012, Elephant management plan. Kruger National Park. 2013–2022, SANParks, Skukuza, South Africa.
- Scholtz, T., 2007, 'The evaluation of the establishment and growth of indigenous trees to restore deforested riparian areas in the Mapungubwe National Park, South Africa', Doctoral dissertation, North-West University, viewed 04 April 2019, from http://hdl.handle.net/10394/1842.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R. & Slotow, R., 2008, 'The utilization of large savanna trees by elephant in southern Kruger National Park', *Journal of Tropical Ecology* 24(3), 281–289. https://doi.org/10.1017/S02664674 08004951
- Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C. et al., 2013, 'Effects of social disruption in elephants persist decades after culling', Frontiers in Zoology 10(1), 62. https://doi.org/10.1186/1742-9994-10-62
- Sianga, K., Van Telgen, M., Vrooman, J., Fynn, R.W. & Van Langevelde, F., 2017, 'Spatial refuges buffer landscapes against homogenisation and degradation by large herbivore populations and facilitate vegetation heterogeneity', Koedoe 59(2), 1–13. https://doi.org/10.4102/koedoe.v59i2.1434
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., Du Toit, J.T. et al., 2004, 'The return of the giants: Ecological effects of an increasing elephant population', AMBIO: A Journal of the Human Environment 33(6), 276–282. https://doi.org/10.1579/0044-7447-33.6.276
- Skarpe, C., Du Toit, J.T. & Moe, S.R., 2014, Elephants and savanna woodland ecosystems: A study from Chobe National Park, Botswana, John Wiley & Sons, London
- Smit, I.P.J. & Asner, G.P., 2012, 'Roads increase woody cover under varying geological, rainfall and fire regimes in African savanna', *Journal of Arid Environments* 80, 74–80. https://doi.org/10.1016/j.jaridenv.2011.11.026
- Smit, I.P., Asner, G.P., Govender, N., Vaughn, N.R. & Van Wilgen, B.W., 2016, 'An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas', *Journal of Applied Ecology* 53(5), 1623–1633. https://doi.org/10.1111/1365-2664.12738
- Smit, I.P.J., Grant, C.C. & Whyte, I.J., 2007, 'Elephants and water provision: What are the management links?', *Diversity and Distributions* 13(6), 666–669. https://doi.org/10.1111/j.1472-4642.2007.00403.x

- Stalmans, M., Attwell, B. & Estes, L., 2002, *Hunting in the Associated Private Nature Reserves. Environmental Impact Assessment Process.* Draft Scoping Report to the Department of Finance and Economic Development (Limpopo Provincial Government), 74 p.
- Stevens, N., Erasmus, B.F.N., Archibald, S. & Bond, W.J., 2016, 'Woody encroachment over 70 years in South African savannahs: Overgrazing, global change or extinction aftershock?', *Philosophical Transactions of the Royal Society B* 371(1703), 20150437. https://doi.org/10.1098/rstb.2015.0437
- Styles, C.V. & Skinner, J.D., 2000, 'The influence of large mammalian herbivores on growth form and utilization of mopane trees, Colophospermum mopane, in Botswana's Northern Tuli Game Reserve', African Journal of Ecology 38(2), 95–101. https://doi.org/10.1046/j.1365-2028.2000.00216.x
- Tambling, C.J., Minnie, L., Adendorff, J. & Kerley, G.I., 2013, 'Elephants facilitate impact of large predators on small ungulate prey species', *Basic and Applied Ecology* 14(8), 694–701. https://doi.org/10.1016/j.baae.2013.09.010
- Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P., 2011, 'Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna', *Biological Conservation* 144(2), 902–912. https://doi.org/10.1016/j.biocon.2010.10.029
- Vanak, A.T., Thaker, M. & Slotow, R., 2010, 'Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore?', *Biological Conservation* 143(11), 2631–2637. https://doi.org/10.1016/j.biocon.2010.07.005
- Van Aarde, R.J. & Jackson, T.P., 2007, 'Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in southern Africa', Biological Conservation 134(3), 289–297. https://doi.org/10.1016/j.biocon.2006.08.027
- Van Aarde, R.J., Jackson, T.P., Guldemond, R.A.R., Kinahan, A.A., De Beer, Y., Shrader, A.M. et al., 2005, 'Elephants and their management in the Kruger National Park', in C.C. Grant (ed.), Elephant effects on biodiversity: An assessment of current knowledge and understanding as a basis for elephant management in SANParks, South African National Parks, pp. 220–223, Scientific Services, Skukuza. Scientific Report 3/2005.
- Van Aarde, R., Whyte, I. & Pimm, S., 1999, 'Culling and the dynamics of the Kruger National Park African elephant population', *Animal Conservation Forum* 2(4), 287–294.

- Van de Water, A. & Matteson, K., 2018, 'Human-elephant conflict in western Thailand: Socio-economic drivers and potential mitigation strategies', *PLoS One* 13(6), e0194736. https://doi.org/10.1371/journal.pone.0194736
- Vogel, S.M., Henley, M.D., Rode, S.C., Van de Vyver, D., Meares, K.F., Simmons, G. et al., 2014, 'Elephant (Loxodonta africana) impact on trees used by nesting vultures and raptors in South Africa', African Journal of Ecology 52(4), 458–465. http://dx.doi. org/10.1111/aje.12140
- Wall, J., Douglas-Hamilton, I. & Vollrath, F., 2006, 'Elephants avoid costly mountaineering', Current Biology 16(14), R527–R529. https://doi.org/10.1016/j. cub.2006.06.049
- Wassenaar, T.D., Ferreira, S.M. & Van Aarde, R.J., 2007, 'Flagging aberrant sites and assemblages in restoration projects', *Restoration Ecology* 15(1), 68–76. https://doi.org/10.1111/j.1526-100X.2006.00191.x
- Western, D. & Maitumo, D., 2004, 'Woodland loss and restoration in a savanna park: A 20-year experiment', *African Journal of Ecology* 42(2), 111–121. https://doi.org/10.1111/j.1365-2028.2004.00506.x
- Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P. & Burnham, K.P., 2014, 'Illegal killing for ivory drives global decline in African elephants', Proceedings of the National Academy of Sciences 111(36), 13117–13121. https://doi.org/10.1073/pnas.1403984111
- Whyte, I.J., 2001, 'Conservation management of the Kruger National Park elephant population', PhD thesis, University of Pretoria, Pretoria, viewed 11 May 2018, from http://hdl.handle.net/20.500.11892/174640.
- Woolley, L.A., Millspaugh, J.J., Woods, R.J., Van Rensburg, S.J., Mackey, R.L., Page, B. et al., 2008, 'Population and individual elephant response to a catastrophic fire in Pilanesberg National Park', PLoS One 3(9), e3233. https://doi.org/10.1371/journal.pone.0003233
- Young, K.D., Ferreira, S.M. & Van Aarde, R.J., 2009, 'Elephant spatial use in wet and dry savannas of southern Africa', *Journal of Zoology* 278(3), 189–205. https://doi.org/10.1111/j.1469-7998.2009.00568.x
- Young, T.P., 2000, 'Restoration ecology and conservation biology', Biological Conservation 92(1), 73–83. https://doi.org/10.1016/S0006-3207(99)00057-9