A systematic review of the success and unintended consequences of management interventions on African elephants

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Abstract

With elephant numbers increasing in some parts of their range, and related conservation concerns including elephants' impact on vegetation and human–elephant conflict, management interventions have been used to artificially reduce elephant numbers, to stabilize populations locally and regionally, or to affect their spatial distribution. Interventions may have environmental, demographic, or social impacts, often unintended. We evaluated elephant management interventions, including both direct (contraception, vasectomy, translocation, hunting, culling) and indirect interventions (fencing, range expansion, corridors, water provision, and fire management). The study draws on evidence from across the range of African and Asian elephants, but with a focus on South Africa, through a systematic literature review using Science Direct, Web of Science, Scopus, Google Scholar, and Google from 2007 onwards, i.e. covering the period since the publication of the 2008 Assessment of South African Elephant Management. We focus on the effects of management on elephants, and present information on success of each method, as well as its demographic effects. We also identified unintended consequences of the interventions, such as increased human–elephant conflict, irruptive growth rates, social disruption, inbreeding depression, truncation of migratory routes, excessive vegetation damage, and breakdown in social structure. Culling and trophy hunting had the most unintended consequences, and evoked the most negative sentiments among tourists. There was a large disparity in the research effort directed towards different interventions, and we highlight gaps where additional research is needed. Elephant management can be contentious, with polarized views, and the broader social and economic elements need consideration. Disservices such as human–elephant conflict need to be reduced, and increased attention paid to animal welfare, and the broader expectations of society in this regard.

Despite the review not being restricted, our study is informed mainly by research carried out in South Africa, drawing in large part on the base created by the 2008 assessment, as well as the norms and standards for management interventions formalized in South African regulations. Furthermore, the aim of the review was to produce information that could be used to update current approaches to elephant management in South Africa. The review draws on publications outside South Africa where they are available, as knowledge gained elsewhere is crucial for improving management decisions. We believe that our study has wider application for use throughout the African savannah elephant range.

Résumé

Du fait du nombre d'éléphants en augmentation dans certains territoires et des inquiétudes relatives à leur conservation — dont les répercussions sur la végétation et les conflits humains-éléphants — des interventions de gestion ont été mises en place afin de réduire artificiellement les populations et les stabiliser localement et régionalement, ou pour agir sur leur répartition dans ces espaces. Des impacts environnementaux, démographiques ou sociaux, souvent imprévus, peuvent découler de ces opérations. Nous avons évalué ces interventions de gestion, qu'elles soient directes (contraception, vasectomie, transferts, chasse, abattage) ou indirectes (clôtures, agrandissement des aires de répartition, couloirs biologiques, approvisionnement en eau ou gestion des incendies). L'étude s'appuie sur des données provenant de l'ensemble des aires de répartition des éléphants d'Afrique et d'Asie avec un gros plan sur les individus sud-africains, grâce à une analyse systématique de la littérature sur le sujet en utilisant Science Direct, Web of Science, Scopus, Google Scholar et Google à partir de 2007, soit toute la période depuis le 2008 Assessment of South African Elephant Management (Évaluation de la gestion de l'éléphant sud-africain en 2008). Nous avons ciblé les effets immédiats de ces interventions sur les éléphants et nous présentons ici les réussites de chaque méthode, ainsi que leur impact sur la démographie. Nous avons également identifié les conséquences involontaires de ces initiatives, telles que l'augmentation des conflits humains-éléphants, des croissances soudaines de certaines populations, des perturbations sociales, dépression consanguine, routes migratoires tronquées, dommages excessifs dans la végétation et dégradation des structures sociales. L'abattage et la chasse au trophée ont causé les retombées les plus inattendues et ont suscité les sentiments les plus négatifs parmi les touristes. D'importantes disparités ont été constatées dans l'effort de recherche consacré aux différentes interventions et nous soulignons les lacunes lorsque de plus amples informations sont nécessaires. La gestion des éléphants peut être controversée et soulever des points de vue opposés, et les composantes sociales et économiques plus générales doivent être prises en compte. Il convient de réduire les torts causés par les conflits humain-éléphant et d'accorder une plus grande attention au bien-être des animaux et aux attentes de la société à cet égard.

Bien que le rapport ne soit pas restrictif, notre étude se base principalement sur les recherches menées en Afrique du Sud, plus précisément sur les éléments rassemblés lors de l'évaluation de 2008, ainsi que sur les normes et critères des interventions de gestion formalisés dans la réglementation sud-africaine. De plus, l'objectif du rapport était de produire des informations pouvant être utilisées pour une nouvelle approche de la gestion de l'éléphant en Afrique du Sud. Le compte-rendu fait appel à certaines publications autres que sud-africaines lorsqu'elles étaient disponibles, car indépendamment de leur origine, les données sont essentielles pour renseigner les décisions dans le domaine de la gestion. Nous considérons que notre étude sera utile dans toutes les aires de répartition de l'éléphant de savane.

Introduction

A key tenet of wildlife management is a requirement to assess the effectiveness of past conservation management approaches, as this provides a foundation for improving future effort (Pullin and Knight 2001). This relies on scientific evaluation of the effectiveness of previous approaches in achieving objectives, and then basing future decisions on the resulting evidence (Pullin et al. 2004; Lim et al. 2017). In so doing, conservation management can move away from decision making based on the personal opinions of practitioners or scientific experts, towards science-based management (Pullin et al. 2004). Despite the best intentions of managers, conservation management often has indirect and unintended consequences. The latter are often overlooked when assessing the effectiveness of biodiversity conservation actions, in part because they generally derive from indirect effects, and, therefore, typically take a long time to manifest (Larrosa et al 2016). Unintended consequences can have both positive and negative effects on the overall (net) outcomes of management interventions, and thus significantly affect management outcomes (Larrosa et al. 2016). Negative effects are particularly important from a management perspective, as they can seriously compromise the effectiveness of management interventions. Therefore, for conservation management to be effective, due attention should be given to potential unintended consequences, as these can lead to waste of already limited conservation resources (Primack 2002).

As the largest extant land mammals, elephants have attracted human attention for millennia (Riddle et al. 2010). The African savannah elephant (*Loxodonta africana*) is a highly valued species and has a major ecological influence on savannah dynamics (Kerley et al. 2008), playing significant roles in nutrient cycling and seed dispersal (Dudley 2000; Blake et al. 2009). As a result, elephants are considered as a keystone or flagship species (Shoshani et al. 2004). African elephants (hereafter 'elephants') are water-dependent, bulk feeders that are not very selective, preferring grazing to browsing (van Wijngaarden 1985). However, elephants tend to shift from grazing to browsing in response to seasonal changes in food quality (Codron et al. 2006; Woolley et al. 2009; Kos et al. 2012). Because of their large ecological impacts, elephants are considered as habitat modifiers or ecological engineers (Jones et al. 1994) that physically alter patterns of resource availability in ecosystems, triggering cascading effects on other trophic levels (Smallie and O'Connor 2000; Shannon et al. 2008; Lagendijk et al. 2011). Due to their large body size, the scale of elephant impacts is usually large, with the potential to completely alter ecosystem dynamics (Skarpe et al. 2004), but also disperse seeds and distribute nutrients (Calenge et al. 2002; Kerley et al. 2008). As a result of these behaviours, the vegetation structure can undergo significant changes in terms of tree height, canopy cover and species composition, with consequences for fauna coexisting with elephants (Smallie and O'Connor 2000; Lagendijk et al. 2011).

Across large parts of the African savannah elephant range, early management interventions on elephants were focused principally on manipulating numbers (Pienaar and van Niekerk 1963; Whyte et al. 1998). The provision of artificial water points is an example of a management approach aimed at increasing elephant numbers (Pienaar and van Niekerk 1963; Croze and Lindsay 2011) by buffering populations against potential negative effects of droughts (Pienaar 1983). This can result in large increases in elephant numbers as a demographic response to the increased availability of a limiting resource (Chamaille-Jammes et al. 2007a; Shrader et al. 2010). However, this may pose a problem for management, as the increase in elephant numbers may be detrimental to vegetation, and the conservation of other species (Owen-Smith 1996). In areas where elephant densities are high, tree-dominated (closed) savannahs can be converted to a grass-dominated (open) state (Owen-Smith et al. 2006; Guldemond and van Aarde 2008). This modification, commonly termed 'elephant impact', mostly takes place through elephants toppling whole trees, or pollarding trees by breaking and removing branches from their canopies, and by preventing or reducing recruitment and regeneration (Balfour et al. 2007). Noticeable impacts of elephants on plants are broadly referred to as 'elephant damage' (Campbell et al. 1996). In response, various options (e.g. contraception, vasectomy, translocation, hunting, culling, fencing, range expansion, corridors, water provision, and fire management) have been explored to artificially reduce elephant population densities and stabilize them at levels considered appropriate based on the available resources (van Aarde et al. 1999; Kerley and Shrader 2007) and ecological carrying capacity (ECC). Previously, subjective opinions, not necessarily evidence-based, dominated management approaches to reduce elephant impacts (van Aarde et al. 2006; van Aarde and Jackson 2007). Currently, elephant management approaches are becoming more integrated, with ecological theory being at the epicentre of management decisions (van Aarde and Jackson, 2007; Robson and van Aarde 2018), through promoting ecological processes to regulate elephant numbers naturally (Owen-Smith et al. 2006; van Aarde and Jackson 2007). For example, in many protected areas (PAs) where elephants occur, managers have increased the area available to elephants by dropping fences, while limiting resource availability by closing artificial water points, so that elephant numbers can fluctuate naturally (Owen-Smith et al. 2006; Chamaille-Jammes et al. 2007a; 2007b; Smit et al. 2007a; 2007b; Druce et al. 2008).

A comprehensive assessment of elephant management interventions was published in 2008 as the Assessment of South African Elephant Management (ASAEM) (Scholes and Mennell 2008). However, there has been no comprehensive evaluation of the unintended consequences of different elephant management interventions on ecological systems (Scholes and Mennell 2008; DEA 2014). As already mentioned above, over time, elephant impacts can transform a landscape dominated by large trees into one dominated by thicket areas (Owen-Smith et al. 2006), which could have serious negative consequences for the rest of biodiversity (Skarpe et al. 2004). This, in turn, may affect tourist perceptions of healthy ecosystems. Thus, tourist perceptions of landscapes provide land managers with a window through which they can obtain useful information for balancing wildlife numbers, ecosystem function, and the aesthetic appeal of the habitat. It has been suggested that tourism may play an important role in elephant conservation as generally elephants in popular tourism areas (i.e. PAs) are safer than elephants in places less frequented by tourists (Chiyo et al. 2014). Thus, from a landscape management perspective, management plans predicated on the presence of elephants in landscapes may attract more revenue from visiting tourists and help conservation of elephant populations (Edge et al. 2017). However, this perspective is unlikely to apply in areas where elephants have become overly abundant as their impacts on vegetation could detract from the aesthetic appeal of the habitat, leading to negative tourist perceptions, which can translate into reduced tourism revenues (Edge et al. 2017). The effects of elephants on biodiversity features of landscapes as well as their aesthetic appeal is a key aspect of elephant management that has hitherto received scant attention.

This paper evaluates the success and unintended consequences of various elephant management interventions as provided for in the Norms and Standards for the Management of Elephants in South Africa (SA). We consider interventions that are directed at the elephants themselves, namely contraception, vasectomy, translocation, hunting, and culling (direct interventions), as well as interventions in the landscape that indirectly effect the elephants, namely fencing, range expansion, corridors, water provision, and fire management (DEAT 2008). Among elephant range states, SA is the only country to have promulgated such regulations, which are primarily aimed at management of elephants in areas confined by fencing. While fenced PAs have long existed in other southern African countries, more and more countries in other parts of Africa are erecting fences to constrain movements of elephants to reduce conflicts with people.

While the review draws on literature on these interventions from across the elephants' range, it does not address additional interventions, such as those to manage human–elephant conflict (HEC) in free-roaming elephants moving through human-dominated landscapes. This review does not discuss comprehensive, integrated elephant management approaches, but focuses on the implementation of specific management tools and interventions. We conducted a systematic literature review of published and grey literature on the use of these methods, and their effectiveness (positive outcome) and demographic consequences (whether positive or negative), as well as their indirect effects and unintended consequences. Since a previous comprehensive assessment was published in 2008 (Scholes and Mennell 2008), we focused on literature published since 2007. While the review is based around the South African regulations, we hope that our results and conclusions will be more widely applicable, and inform implementation of these interventions across the range states.

Methodology

A systematic literature search, following the principles of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) method (Moher et al. 2009; O'Dea et al. 2021), was carried out on databases of scientific, peer-reviewed literature, followed by manual searches on Google for relevant papers, theses, and grey literature. Firstly, Science Direct, Web of Science, and Scopus databases were searched for published articles on elephant management interventions. All types of research articles (review articles, research articles, book chapters, etc.) were included in the search. The following keywords and Boolean operators were entered separately in combination with the word "elephant", into the databases to retrieve relevant publications,: "AND contraception", "AND vasectomy", "AND water provision", "AND fire", "AND fencing OR fence", "AND corridor OR connectivity", "AND range expansion", "AND translocation", "AND culling OR hunting", or "AND tourism OR tourist experience" (11 different search combinations). Articles relating to each management strategy were searched for separately, with the number of hits generated recorded at each time. This study follows up on the ASAEM (Scholes and Mennell 2008) published in 2008, and the search period was set to 2007–2021 so as to pick up all relevant literature not evaluated by the initial assessment. The search of the relevant literature was conducted in April 2019, with another updated search conducted in October 2021. Papers whose titles included any of the key words were retained for inclusion in the review. However, as using only the title as a selection criterion may miss potentially useful articles, the abstract of articles that came up in the search whose titles did not contain the key words were also read to confirm their relevance to the topic. Finally, a search was conducted for literature reviews and meta-analyses on the subject, in order to source relevant publications that were missed in the initial search.

For an article to be included in the initial phase of the elimination process, it had to present results of the application of a particular management intervention in the field (studies conducted on captive elephants were not considered) and to be published in the English language. Conceptual/modelling articles and reviews were, however, retained. To increase the comprehensiveness of the review, in addition to articles on the savannah elephant (*Loxodonta africana*), articles on the African forest elephant (*L. cyclotis*) and the Asian elephant (*Elephas maximus*) were also retained. After following these steps, a total of 221 publications were identified and retained.

Additional searches were conducted to uncover potentially eligible published work that was missed by the database search. In this study, the Reference sections of all articles considered suitable for inclusion were read to identify: 1) potentially relevant articles; and 2) journals which frequently publish relevant studies. Potentially relevant articles were then manually searched using the Google Scholar search engine. An additional 90 articles were added to the database following this step.

Journals were also manually searched to identify articles (and other work, e.g. letters, comments, notes, opinions) which had not yet been included in electronic databases, and those which were not indexed, or indexed incorrectly, but that met the criteria for inclusion listed above. There were 19 additional articles included in this step; however, these publications were flagged as not peer-reviewed, and any information was included with caution.

Although systematic reviews aim to be as comprehensive and representative of the literature as possible, publication bias can still occur when not all authors submit their results for publication (Borenstein et al. 2009; Lipsey and Wilson 2001). A reason frequently given for excluding unpublished research from systematic reviews is that it is often of lesser quality than published research (Borenstein et al. 2009; Corlett 2011). However, some research associated with degree requirements is conducted by individuals who do not seek academic careers (authors' *pers. obs.*). Moreover, many research programs are conducted as evaluations for agencies making internal decisions about program effectiveness, and such research typically never gets published (Cooper 2003). Also, research is often turned down for publication for reasons other than quality, such as the failure to obtain results that reject the null hypothesis (Cooper 2003). Thus, a search was conducted for unpublished work (conference papers, reports, abstracts, newspaper articles, project reports, social media posts, etc.) using Google search. Thirty-one (31) articles were identified in this manner, and labelled as grey literature, and included with the necessary caution.

To search for postgraduate theses, online theses databases at universities were visited and searched. Firstly, for each thesis that came out in the original search using the search terms for the review, we noted the institution where the corresponding post-graduate degree was awarded, and then compiled a list of these institutions. We then investigated (mainly by sending emails to administrative staff) whether the institution concerned has an online database where theses are available for download. If so, we searched for the thesis of interest and downloaded it. We further searched for other theses on elephants in the database using the search term "elephant". For universities where theses were not available for download, emails were sent to the authors to request copies. To increase the comprehensiveness of the search, further searches were conducted on Google using phrases such as "MSc or PhD thesis on elephants". Thirty-five (35) theses with additional information that was not published in the peer-reviewed literature were included.

All of these searches yielded a total of 306 publications for inclusion in the review. Duplications were then excluded (19), resulting in a total of 287 publications. The remaining publications were then read and assessed for eligibility, of which 104 were removed for not meeting the criteria for inclusion, leaving a total of 183 publications. Of these, 148 were published research papers, 24 were unpublished theses, and eight were unpublished material (conference papers and project reports).

Selected publications were read and any information about the implementation of the technique, the success or not in achieving the intended outcome, and demographic responses (intended or unintended), and/or any unintended consequences was extracted for inclusion in the review. Extracted information was summarized and populated into a Microsoft Excel sheet for ease of reference.

Results

A total of 183 publications met our criteria for inclusion. Amongst these, an overwhelming majority (71%) were experimental/research papers and reviews/conceptual papers (16%), while only a few were theses (7%) and grey literature/project reports (6%) (Table 1).

Birth/population control through contraception or vasectomy

Due to the controversy associated with lethal elephant management approaches, non-lethal control measures are being increasingly sought and utilized (Garai et al. 2018). Birth/population control is now considered an important alternative avenue for controlling South Africa's increasing elephant population (Fayrer-Hosken et al. 2000), and has been incorporated into the Norms and Standards as an approved intervention to control population size and distribution of elephants since 2008 (DEAT 2008). Four methods of contraception have been explored for elephants, three of which are applied to females, including estrodiol treatment, immunocontraception with porcine zona pellucida (pZP) and, more recently, immunocontraception using gonadotropin-releasing hormone (GnRH) (Bertschinger et al. 2008, Bertschinger and Caldwell 2016, Delsink et al. 2013; Garai et al. 2018). For males, two methods of contraception are available: the use of GnRH and vasectomy (Bertschinger et al. 2008, Bertschinger and Caldwell 2016, Lueders et al. 2017). The various contraception options for elephants are reviewed in Chapter 6 of the 2008 elephant assessment (Bertschinger et al. 2008).

The results of estrodiol treatments of 10 cows in Kruger National Park (NP) are summarized in

Table 1. Summary of number and types of research publications on elephant management interventions

Topic	Number of papers in initial search	Number of publications retained	Experimental	Reviews/ conceptual	Theses	Grey literature
Birth control (contraception and vasectomy)	309	32	16	9	4	3
Corridors	253	28	24	0	2	2
Culling	192	10	8	1	0	1
Hunting	27	6	6	0	0	0
Fencing	407	22	6	14	2	0
Range expansion	350	9	4	5	0	0
Translocation	380	23	20	0	3	0
Water provision	430	45	38	0	2	5
Fire management	231	4	4	0	0	0
Tourism	189	4	4	0	0	0

Bertschinger et al. (2008), where cows did not fall pregnant for a year, but, unfortunately, they were in oestrus for 12 months, which created behavioural problems in the herds. This option was discontinued and is no longer considered a safe choice for contraception of elephants (Bertschinger et al. 2008).

Among the remaining methods, immunocontraception is considered the least invasive way of controlling elephant fertility, and has shown the most promise (Delsink and Kirkpatrick 2012). As a non-hormonal measure, immunocontraception is less likely to lead to problems associated with hormonal imbalances, which can lead to aggressive behaviours, especially among bulls (Fayrer-Hosken et al. 2000). This method relies on inducing immune responses to specific proteins (antigens) that are involved in critical stages of animal reproduction. When these antigens are injected into the body, they cause a release of antibodies which either neutralize the antigen or block a process such as fertilization (Bertschinger and Caldwell 2016; Bertschinger et al. 2018). The pZP vaccine works by binding with zona proteins which surround the oocyte of the female, thereby blocking sperm-zona binding, thereby preventing of fertilization from taking place (Bertschinger and Caldwell 2016). The GnRH vaccine induces antibodies which neutralize GnRH in the target animal, blocking the ability of this hormone to stimulate gonadotropin release from the adenohypophysis in both males and females (Bertschinger and Caldwell 2016).

The first case of pZP application in free-ranging elephants in South Africa was conducted in the Kruger National Park in 1995 (Fayrer-Hoskin et al. 2000). Treatment of elephants with pZP was found to successfully control their birth rates, with reported efficacies of up to 80% (Delsink et al. 2007). Even better results were obtained in the Greater Makalali Private Game Reserve (GR), with pZP demonstrated to be 100% effective in reducing population growth, with no calves born (Delsink et al. 2006; Bertschinger and Caldwell 2016). In a long term pZP application programme in Makalali, both the effectiveness and the reversibility of the pZP technique were confirmed (Delsink et al. 2013). Initially, the efficacy of the approach for large populations, where individuals cannot be individually marked, was questioned (Kerley and Shrader 2007). However, pZP has been applied in a number of larger populations (Druce et al. 2011; Bertschinger et al. 2018). Aerial administration of the pZP vaccine reduces the need to individually monitor each elephant, and to hire people to do that, thus making the procedure feasible even for large populations (Delsink et al. 2007). Furthermore, administration of pZP from helicopters makes the method very time-effective, allowing elephants in small populations to be contracepted in 30 minutes (Delsink and Kirkpatrick 2012). In 2017, pZP was applied to 811 cows across 27 reserves, with 34 reserves in SA having participated in the programme over the years (Nolan 2019).

At the time of the elephant assessment (Bertchinger et al. 2008), GnRH was emerging as a potential option for contraception in both male and female elephants, but little work had yet been done. Since then, studies have been published on the use of GnRH on both wild and captive elephants (for reviews see Bertschinger and Caldwell (2016; Bertschinger and Lueders 2018). GnRH has been shown to contracept male elephants, effectively acting as a chemical castration (Bertschinger and Caldwell 2016, Lueders et al. 2017, Bertschinger and Lueders 2018). In terms of female contraception, Valades et al. (2012) reported that GnRH was not able to induce anoestrus in wild female elephants. Subsequently, increasing the dosage to 1000 mg has shown success in inducing anoestrus in captive females (Bertschinger and Lueders 2018). We are aware that GnRH has been used for both males and females in a number of reserves and captive populations; however, the results have not yet been reported in the literature (see also Bertschinger and Caldwell 2016). Currently GnRH is used more to manage the behaviour of problem male elephants (see Bertschinger and Caldwell 2016, Bertschinger and Lueders, 2018) rather than for contraception, with PZP used for the contraception of females.

Vasectomy is another potential elephant population management approach (Zitzer and Boult 2018). Among 45 free-ranging elephants in SA subjected to vasectomy in seven nature reserves, one died and two others had surgery complications, but recovered and showed no abnormal behaviour (Marais et al. 2013). In another study, large intestine lacerations (a common occurrence in vasectomies and castration) were seen after vasectomy; however, the elephants healed without any incident (Rubio-Martinez et al.

2014). Overall, it appears that vasectomy can be implemented on wild males with no serious complications in anaesthesia, during surgery, or in the postoperative period (Marais et al. 2013). While vasectomies have been performed on bulls up to 40 years old (Marais et al. 2013), it may be challenging to vasectomize older males, as vets could not find the vas deferens in a 40 to 45-year-old male because of fat deposits around the testes (Zitzer and Voult 2018). The main advantage of this procedure is that it has to be done only once, whereas with immunocontraception, animals have to be treated several times, raising costs as well as the levels of stress the animals are subjected to (Marais et al. 2013; Rubio-Martinez et al. 2014). Vasectomies have, to date, only been applied in reserves with few adult males, and, in at least two, new calves were born, presumably sired by younger bulls (Doughty et al. 2014; Nolan 2019).

Demographic responses to contraception

Non-lethal control methods are considered to be more effective than lethal methods (see below) as they do not directly reduce population numbers but rather lower the reproductive rate (Delsink et al. 2006). Modelled effects of immunocontraception over a period of 20 years of application showed that it can reduce elephant population growth rates by up to 64% (Mackey et al. 2009). Indeed, field studies have found significant declines in population growth rates after immunocontraception application. For example, after 22 months of pZP application, no pregnancies were reported in the elephant population in Thornybush Private GR, SA (Ahlers et al. 2012). In small GRs, where cows can be individually vaccinated, the pZP vaccine was found to be 100% efficient in reducing population growth rate (Bertschinger and Caldwell 2016), an efficacy level never recorded before in any free-ranging species (Kirkpatrick et al. 2011). Even in larger elephant populations, high levels of efficacy (>95%) have been observed (Bertschinger et al. 2018). However, increased use of contraception will result in an aging population, in which females become dominant (Bertschinger et al. 2008).

There is no study, to our knowledge, that assesses demographic responses to vasectomy or GnRH. However, given that calving has been observed to occur after dominant males were treated with GnRH or vasectomized (Doughty et al. 2014), the demographic effect of these treatments is likely to be minimal unless they are applied to all mature males in a population (for vasectomy, see Garai et al. 2018). If all males are contracepted or vasectomized, this will lead to an aging population.

Unintended consequences of birth/population control

Two opinion papers in 2007 raised concerns over the potential unintended consequences of contraception (Kerley and Schrader 2007; Perdock et al. 2007). Kerley and Schrader (2007) raised concerns based on their understanding of elephant biology, and not on any evidence collected from contracepted females, which included: physical harm to adult elephants from males pursuing females in oestrus, or fighting over adult females; the absence of calves reducing herd cohesion, and families without calves joining others, creating larger herds; calves from first-time mothers having greater mortality; calves potentially suffering fatal harassment from females without calves; mothers distracted from feeding and producing less milk, leading to calf mortality; kidnapping of calves increasing; more male bias in offspring; contracepted females changing their ranging behaviour, becoming less selective in food choices, and altering their ecological impact.

Perdock et al. (2007) were concerned over some potential long-term effects, including that contraception would favour weaker animals; and that immunity to vaccine may arise. They also raised concerns over reversibility, lack of young in the herds, ongoing oestrus among females affecting male behaviour, and effects of repeat darting (making elephants more wary or nervous). Kerley and Schrader (2007) note that contraception requires repeated treatment of animals; up to 75% of animals would need to be contracepted annually to achieve negative population growth; and that contraception would not reduce population size in the short term.

When injected into pregnant elephants, pZP has no negative effects on the foetus, on gestation or on parturition (Bertschinger et al. 2008). Thus, pZP appears to cause no harm to the pregnant females or foetuses at any stage of their development (Bertschinger et al. 2018), suggesting that it is unlikely to have negative effects when applied inadvertently on already pregnant females. Furthermore, the vaccine can be delivered remotely, without the need for immobilization or animal capture (Bertschinger et al. 2018). An 11–year study in the Greater Makalali Private GR found that contraception did not have long-term effects on social or spatial aspects of elephant behaviour (Delsink et al. 2013). Furthermore, it had no effect on male–male competitive interactions or female mate choice (Delsink et al. 2013). At Phinda Private GR, South Africa (SA), the disruptive effect of immunocontraception darting on the family groups within the population was minimal, with no significant changes found in the mobility of family groups (Druce et al. 2013). There was no significant relationship between bulls' association with family groups and the number of oestrous females present in the group (Druce et al. 2013). At Thornybush Private Nature Reserve (NR) SA, two years after the initiation of pZP vaccination, eight of the 14 elephant females exhibited a cyclic pattern: two exhibited an irregular cyclic pattern lasting longer than is natural, while the remaining six underwent at least one complete oestrus cycle (Ahlers et al. 2012). Furthermore, elephants showed a lack of anoestrus, suggesting pZP does not interfere with normal follicular development and ovulation, in a study that took place during a drought, which reduces body condition and normally increases anoestrus (Ahlers et al. 2012).

Nevertheless, the limited knowledge of elephant reproductive behaviour makes it difficult to determine the unconfounded effects of pZP on elephants (Ahlers et al. 2012). One issue with pZP vaccination is that boosters are necessary to maintain the effects of contraception, which may increase the costs associated with this procedure (Delsink et al. 2013). Nevertheless, from years of application to wildlife, the pZP vaccine appears to come reasonably close to displaying the characteristics of an ideal wildlife contraceptive (sensu Kirkpatrick and Turner 1991; Berchert and Fracker 2016). These include remote delivery, contraceptive reversibility, safety in pregnant animals, lack of behavioural effects, no passage through the food chain, no debilitating long-term health effects, relatively low cost, and at least 90% efficacy (Kirkpatrick and Turner 1991; Kirkpatrick et al. 2011). Note that, although medium-term studies indicate reversibility, the effect of application for more than a decade on reversibility is not known (Garai et al. 2018). Garai et al. (2018) indicate that physical effects of pZP are unclear; however, neither of the only two post-mortems conducted on contracepted females found evidence of adverse pathology.

An unintended population level consequence of pZP immunocontraception could be an increased adult female to male ratio due to disproportionate male mortality from various causes (Bertchinger et al. 2008). An intended or unintended consequence of population-level pZP immunocontraception is an aging population (Bertchinger 2008); importantly, the subsequent increased population-level mortality from senescence would contribute to the goal of long-term population reduction, but this should be planned for so that it is understood as an intended result of management. In populations where all females are continually contracepted, the absence of calves may change social behaviour, and this, as well as any long-term demographic effects, should be investigated. Ideally, provision should be made for some births to take place in the population. There may be unintended effects of pZP immunocontraception on genetic diversity, and monitoring and research on this is required (Bertschinger et al. 2008).

GnRH, on the other hand, is associated with a number of problems, including acute swelling and inflammation post-surgery (Lueders et al. 2014). GnRH was not developed to be reversible, and the threshold application level at which it will produce permanent infertility males is unknown (Lueders et al. 2014). Furthermore, in the captive Asian elephant, reduced testosterone due to GnRH administration resulted in reduced muscle gain, which may affect the ability of elephants to defend themselves, and to handle and mate with females (Lueders et al. 2014). The effect on bone density also needs to be investigated (Lueders et al. 2017). However, the main problem with GnRH is that, when applied to males, it represents a non-surgical castration, raising issues with regards to reversibility (Kirkpatrick et al. 2011). Moreover, GnRH application to pregnant females may lead to abortion, given that elephants rely on the luteinizing hormone (LH) for maintaining corpus luteum during pregnancy (Kirkpatrick et al. 2011). In males, GnRH also causes significant reduction in testosterone levels and other androgens, and also leads to decreases in testicular and accessory organ sizes (Garai et al. 2018). The ultimate result of this is the feminization of males, if they are treated before reaching puberty (Garai et al. 2018). Consequently, the vaccine should not be administered to near pubertal bulls as it could lead to permanent suppression of reproductive organ development (Bertschinger and Lueders 2018). Doughty et al. (2014) studied the behavioural responses of elephants treated with GnRH in Pongola GR, SA, and found that, following a decline in elephant births after treatment, males were spending more time with female herds, leading to more harassment of females. While the vaccine was applied to dominant males, the authors also found that calving continued to occur in the population, suggesting that subordinate sub-adults were fathering the calves, raising concerns about the future fitness of the population (Doughty et al. 2014).

Other troubling issues have emerged with the use of vaccines that block GnRH production in other species. For example, it has been demonstrated that GnRH receptors exist in various tissues throughout the mammalian bodies, including the cerebellum, bladder, and the cerebrospinal fluid (Bahk et al. 2008). Thus, GnRH has physiological effects throughout the central nervous system, suggesting that unintended outcomes are likely to affect a range of bodily functions, with serious consequences for individual health and reproduction (Kirkpatrick et al. 2011). Moreover, GnRH activity can affect olfactory function (Kirkpatrick et al. 2011), which is an important part of the reproductive process in many species. In the cerebral cortex, GnRH can lead to depressed activity, and, in the cerebellum, GnRH has been linked to two genetically-based disorders; Gordon–Holmes Syndrome and Boucher–Neuhauser Syndrome (Kirkpatrick et al. 2011). cardiac tissue has a high concentration of GnRH receptors, and GnRH can have a serious negative impact on cardiac function in male humans, blocking GnRH production can increase the risk of coronary infarction (Schofield et al. 2002). Whether or not these issues have clinical relevance for free-ranging elephants is still unknown, but the fact that GnRH exerts its influence far 'upstream' in the reproductive process, raises issues concerning target tissue function; more so than with vaccines that exert their effects further 'downstream' in the reproductive process (e.g. pZP). Furthermore, the consequences of younger males becoming dominant (Slotow et al. 2000) as a result of GnRH treatment of dominant males are unknown, but could be important (Doughty et al. 2014; Garai et al. 2018).

Vasectomies are not known to affect the behaviour of treated males, although the reversibility of the approach is yet to be determined (Garai et al. 2018). Lacerations in the large intestine occurred after vasectomy in some elephants, but these healed without any incident (Rubio-Martinez et al. 2014). Moreover, this is not only an issue with vasectomy, as accidental intestinal lacerations are a common occurrence following other similar surgeries such as castration (Rubio-Martinez et al. 2014). Further studies confirm that elephants subjected to vasectomy recovered quickly and showed no abnormal behaviours, suggesting that the procedure causes no anaesthetic, surgical and postoperative complications (Marais et al. 2013; Zitzer and Voult 2018). If only dominant males, and not all mature males, are vasectomized, sub-adult males may succeed in breeding (Garai et al. 2018), which may reduce population fitness (Doughty et al. 2014). If all males are vasectomised (or contracepted with GnRH), this will lead to an ageing population, and may result in social problems for herds experiencing 'calfless-ness' for extended periods.

Translocation

Translocation means the removal by human and mechanical means of a wild elephants from one location to another (DEAT 2008). Translocation has been used for a wide range of wildlife management applications, such as reducing human–wildlife conflicts, reintroducing rare species, and reintroducing species to former ranges (Fischer and Lindenmayer 2000). In southern Africa, the main aim of elephant translocation is to reduce numbers of over-abundant populations in order to reduce negative ecological impacts (Grobler et al. 2008). In other parts of the world, such as East Africa and Asia, elephant translocation is restricted to individuals, usually problem elephants (i.e. those that repeatedly raid crops and cause damage to property or human life) (Fernando et al. 2008; Pinter-Wollman 2009; Fernando 2015). Occasionally, elephant translocation is used to remove small groups isolated within developed landscapes (Fernando et al. 2008). For example, as a result of the increase in agricultural and infrastructural development, elephant populations may become 'pocketed elephant herds'

(Daim 1995). These herds are confined within ecological islands and/or isolated habitats, which represent 'leftovers of development', and are unlikely to be viable in the long term (Daim 1995). Limited home range size, low food availability, and unfavourable habitat conditions cause these elephants to encroach into surrounding farmland, as there are no corridors through which they can move safely and free from human disturbance (Daim 1995). Translocation has been proposed to avert these problems (Wambwa et al. 2001). In addition, when elephants are restricted into a limited area, their impact on the vegetation is likely to increase, and translocation has been used to lessen this impact by reducing population size (Grobler et al. 2008; Morrison et al. 2018).

Another use of elephant translocation is to improve the age structure of the population (Slotow et al. 2000). For example, Slotow et al. (2000) found that young male bulls exhibited a heightened and prolonged state of musth when older bulls were not around to suppress their musth patterns. These bulls exhibited aggressive behaviours towards other species, especially rhinos. The introduction of older males to reduce the duration and onset of musth has thus become an established intervention to reduce the occurrence of these abnormal behaviours (Slotow et al. 2005). Translocation was reviewed as part of the South African elephant assessment (Grobler et al. 2008). The techniques are well known and documented, and it is a relatively routine procedure (Grobler et al. 2008).

Demographic responses to translocation

Although translocation is ethically appealing, this approach is not considered a practical solution to reduce elephant numbers in large populations, because translocation is expensive and cumbersome to conduct (Daim 1995). Moreover, there are few areas in southern Africa in a position to accommodate extra elephants (Whyte 2004), and translocation of elephants across continents raises a range of ethical and logistical issues (Wambwa et al. 2001). Furthermore, populations founded on translocated individuals tend to show abnormal population structures (e.g. unbalanced sex ratios, disproportionately high proportions of adults and sub-adults, etc.) (Slotow et al. 2005). Slotow et al. (2005) studied introduced elephant populations across South Africa and found that these populations reproduced at rates far above average. Similarly, Kuiper et al. (2018) found that introduced/translocated elephants in Hluhluwe-Imfolozi Park showed rapid (exponential) population growth, with the elephant population size doubling every 10 years.

Unintended consequences of translocation

During translocation, animals are inevitably subjected to chronic stress (where the stress response system is pushed beyond normal levels such that it becomes dysregulated) (Dickens et al. 2010). When an animal is exposed to chronic stress levels, the physiological and behavioural responses to stress cease to be beneficial, and become detrimental to survival (Dickens et al. 2010). Chronic stress can cause immune system suppression, changes in cardiac function, and reduced ability to respond to threats, as well as disrupting the reproductive hormone axis and reproductive behaviour (Teixeira et al. 2007; Dickens et al. 2010). Chronic stress does not prevent translocation; however, it is a consequence of the translocation process (Dickens et al. 2010). Moreover, stress may increase the vulnerability of individuals to other stressors, such as disease, predation or starvation. This, in turn, may result in translocation failure, through decreased reproductive capacity or dispersal away from the release site (Teixeira et al. 2007; Hambrecht et al. 2020). During translocation, faecal glucocorticoid levels increase significantly, indicating stress (Millspaugh et al. 2007; Viljoen et al. 2008; Fanson et al. 2013; Viljoen et al. 2015). Fanson et al. (2013) found variation among individuals in hormonal responses to stress, with individuals with a pre-existing high basal faecal glucocorticoid concentration showing a prolonged elevation of faecal glucocorticoid production following release. The authors found that the behavioural traits ('personality' types) of individuals affected their responses to stress associated with translocation: 'social' elephants showed a smaller increase in faecal glucocorticoid concentrations than 'reclusive' individuals (Fanson et al. 2013).

Another issue with translocation of elephants is 'homing' behaviour, whereby translocated individuals return to the initial capture site (Fernando 2015). On their return journey, individuals may experience stress as they move over unfamiliar territory (Hambrecht et al. 2020), and there have been reports of aggressive behaviour which resulted in human deaths (Fernando, 2015). This suggests that, for translocation to be effective, elephants must be transported a large distance away from the capture area. However, studies conducted in Sri Lanka and Kenya report that all translocated individuals left the areas they were translocated to, with some returning to a capture site more than 100 km away (Pinter-Wollman 2009; Fernando et al. 2012). Furthermore, some of these translocated elephants spent some time wandering about in the release site, and many moved into adjacent highly populated areas, elevating the level of HEC there (Fernando et al. 2012; Fernando 2015). The longest documented homing distance made by an elephant was approximately 300 km from an elephant translocation in South Africa (Viljoen et al. 2015). In addition, translocated elephants have been shown to kill a far more people than non-translocated elephants, and, consequently, they also experience a higher mortality rate (Fernando et al. 2012; Fernando 2015). Thus, it appears that translocation, instead of solving HEC, amplifies it and spreads it over larger areas, compromizing both HEC mediation and elephant conservation (Fernando et al. 2012).

Jachowski et al. (2013b) studied the physiological responses of reintroduced elephants in five reserves in South Africa. Elevated stress hormone levels were reported in these elephants even 24 years after the initial release, suggesting that, following release, animals require a long period to acclimatize to the new conditions (Jachowski et al. 2013b). Elephants with elevated stress responses were shown to use a smaller part of their home range than non-stressed ones, confining their movements to within areas they identify as safer 'refugia' for extended periods, suggesting that stressors were likely persistent (Jachowski et al. 2012). Thus, chronic stress leads to reduced space use and altered habitat preferences in elephants, which can affect their nutritional state (Jachowski et al. 2012). Furthermore, one young elephant was reported to have died following release, likely due to the stress associated with translocation, and long, continuous movements of the family group after release (Jachowski et al. 2012). Elephants with an elevated stress response exhibit 'refuge behaviour' (Woolley et al. 2008b; Jachowski et al. 2012), which can affect their ecology, worsen tourist viewing experiences, lead to aggressive encounters with humans (Jachowski et al. 2012), and cause extensive habitat degradation (Lagendijk et al. 2011). There is also a risk of breakout from the reserve, after release, especially if the translocated elephants are not used to electric fences (Grobler et al. 2008). (The translocated elephants are free to roam across the whole reserve, but they select some areas where they feel safer, and use these as refuge areas when stressed. The refuge areas are not fenced and are part of the larger reserve.)

Another cause for concern associated with elephant reintroduction is the increase in vegetation damage at the release site. Studies of the responses of plant populations to elephant reintroduction in Venetia–Limpopo Nature Reserve, South Africa (O'Connor and Page 2014; O'Connor 2017) found that, following elephant introduction, elephants accounted for more than 63% of tree loss (O'Connor 2017). Uprooting, pollarding and ring barking were the main elephant impacts leading to tree mortality. One population of trees was completely eliminated, with many others remaining vulnerable to extirpation due to high adult tree mortality and poor regeneration (O'Connor 2017). Furthermore, elephant impacts completely changed the plant community, which shifted towards dominance by species that can regenerate rapidly to compensate for high mortality, resulting in a simplified community structure (O'Connor 2017). Thus, composition, structure and diversity of woody vegetation was transformed by elephant impacts, leading to a less complex natural community (O'Connor and Page 2014; O'Connor 2017; Howes et al. 2020). In an enclosure experiment at Phinda, reintroduced elephants, in combination with Nyala (*Tragelaphus angasii*), strongly reduced recruitment of threatened sand forest species (Lagendijk et al. 2011). The only behavioural study of elephants on the donor reserve from which they were translocated detected no unintended consequences from two removals of family groups (Druce 2012).

Hunting

In the South African context, there are various types of elephant hunting, including trophy hunting by international/local clients, commercial hunting by South African residents (often, but not always of problem animals), and hunting for non-commercial purposes by the owner or manager of the elephants.

Trophy hunting of elephants has been used to reduce elephant numbers in over-abundant populations, but primarily to generate financial revenue, including for surrounding rural communities (Burke et al. 2008; Mbaiwa 2018; Di Minin et al. 2021a). Trophy hunting can become more profitable than tourism when fees for hunting are high (de Boer et al. 2007). However, there are concerns about whether trophy hunting revenue can provide adequate, long-term benefits to communities, and over inequity in the distribution of money (Dellinger 2019; Di Minin et al. 2021a; Wasser and Gobush 2019). Trophy hunting may not be able to offset the costs of coexisting with elephants (e.g. injury or death, crop losses, or infrastructure damage) (Drake et al. 2021).

Demographic responses to hunting

Trophy hunting of males is an inefficient mechanism to reduce population size and is more appropriate for other management objectives such as removal of problem animals (Slotow et al. 2008). Trophy hunting results in high ratios of females relative to males due to selective hunting of lone bulls resulting in depressed levels of fecundity, due to insufficient male breeding capacity (Selier et al. 2014; Puyravaud et al. 2017).

Unintended consequences of hunting

Burke et al. (2008) studied the behavioural and physiological responses of elephants to trophy hunting in Pilanesberg NP, South Africa. The authors found no significant behavioural responses to hunting or significant changes in the occurrence of elephant breakouts or attacks on infrastructure (Burke et al. 2008). Initially, elephants exhibited a heightened flight response (i.e. they moved away from the hunting area), but their movement stabilized by the next day (Burke et al. 2008). Selier et al. (2014) also found that both male and female elephants moved out of the areas where hunting occurred, and females took longer to return to the area than males. Moreover, elephants subjected to hunting exhibited increased stress hormone levels, even those not directly affected by hunting, suggesting that the stress was transmitted from stressed individuals to the rest of the population (Burke et al. 2008). Although Burke et al. (2008) found that these effects were not strong enough to elicit strong behavioural responses the authors suggested that bulls should be hunted alone in order to minimize any negative effects (Burke et al. 2008). Garaï et al. (2022) found higher negative welfare indicators in a reserve where hunting takes place, although the reserve also has high tourism levels, and they suggest that additional research is required. McComb et al. (2001) demonstrated that elephants responded as if to a threat to playbacks of recorded voices of Maasai men, who traditionally hunted elephant, than to voices of Maasai women or boys, or other ethnic groups that never hunted elephants (see also https://www.nature.com/articles/nature.2014.14846). Selective removal of older males leads to reduction in tusk size (Chiyo et al. 2015; Muposhi et al. 2016), or tusklessness (Whitehouse 2002), which may impact negatively on ecotourism in adjacent areas (Selier et al. 2015), distort the male dominance hierarchy, and reduce genetic fitness (Slotow et al. 2008). A final welfare issue to consider is that achieving "clean/outright" kills is difficult, even in controlled hunting situations (Slotow et al. 2021).

Culling

The ASAEM reviewed the history of culling, the methods used, the economics of possible exploitation of tusks, elephant feet, tails and hides, as well as challenges and consequences of culling (Slotow et al. 2008). For a long time, managers of reserves in many parts of southern Africa advocated culling as a management tool for elephant populations confined to PAs (van Aarde et al. 1999). For example, in SA's Kruger NP, between 1967 and 1994, culling remained the principal management strategy for maintaining the elephant population around a set population size (~7,000 individuals) in order to avert the destruction of vegetation at high elephant densities (Owen-Smith et al. 2006). Nevertheless, increasing public pressure, and lack of unequivocal evidence of the damaging effects of high elephant densities on vegetation, resulted in culling being temporarily discontinued in Kruger NP in 1995. The Minister of Environmental Affairs and Tourism convened a Scientific Round Table to consider the matter in 2006, which concluded culling was not necessary in Kruger NP (Owen-Smith et al. 2006). The Norms and Standards for the management of elephants in South Africa (DEAT 2008) provide for culling as a management option of last resort for reducing or maintaining elephant populations, but not for influencing the spatial distribution of elephants. Despite the conclusions of the Scientific Round Table (Owen-Smith et al. 2006), and the prohibition on the use of culling to influence the spatial distribution of wild elephant populations (DEAT 2008), the current Kruger NP Elephant Management Plan indicates "SANParks will, at appropriate places, implement: … Lethal induction of spatial and temporal variation in elephant numbers (e.g. culling) (Ferreira et al. 2013). Proposed methods to induce spatial variation include "lethal shooting, helicopter shooting, and elephant pitfalls" ("Establish traditional elephant pitfalls in areas of concern. Distress calls must be allowed to be uttered"). (Map 8, Table 4 and Box 15 in Ferreira et al. 2013). Culling, therefore, remains a contentious issue, with discrepancies between what managers propose to do (Ferreira et al. 2013), and what scientists deem necessary (Owen-Smith 2006), or society deems acceptable (DEAT 2008). The issue of culling brings up other related issues such as the continent-wide decline in elephant numbers and proposal for lifting of the ban on ivory trade, which complicates the debate even further (Dickson and Adams 2009; Biggs et al. 2017). In several East African States and Asia, culling is considered an unacceptable elephant management strategy, reflecting cultural attitudes in these regions and the lower number of elephants, although the killing of elephants for crop raiding was formerly considered acceptable in Asia (Fernando et al. 2008). When translocation, capture and domestication, or capture and semi-captive management of Asian elephants are not options, culling may be considered a better and more humane management approach than deaths of elephants at the hands of enraged farmers (Fernando et al. 2008); but see Slotow et al. (2021) for counter arguments. Consequently, culling is generally considered as the last option among elephant control measures (Koenig 2007; DEAT 2008). Many elephant specialists are, moreover, sceptical about culling, as it fails to limit elephant numbers in the long run (Koenig 2007; Slotow et al. 2008).

A recent evaluation of the legal context for culling concluded that the method of culling family groups by first killing the matriarch, and then subsequent group members with the youngest last, is likely inhumane. This method is illegal in South Africa (Slotow et al. 2021). Although this has not yet been tested in court, legal costs and reputational risks may also be considered a potential unintended consequence affecting organizations that implement culling. It should be noted that, although the option of culling of family units to control elephant populations is retained in some management plans in South Africa, such culling has not been carried out since 1995 (R. Slotow, *pers. obs.*). Consequently, a moratorium has been recommended on culling of elephant family units, as well as of lone bulls, be put into effect until more humane methods ensuring an extremely high probability of instantaneous kill are available and approved by the regulatory authorities (Slotow et al. 2021).

Demographic responses to culling

Culling is the only intervention that can directly and substantially reduce population size in the short term; however, it leads to irruptive growth when culling is stopped (Slotow et al. 2008), as the predominance of young elephants in the population, and relatively high availability of resources, allow reproductive rates to increase (van Aarde et al. 1999; Slotow et al. 2008, Mackey et al. 2009). Thus, lethal population control methods (e.g. culling), in addition to their controversial nature, are ineffective in reducing elephant numbers without future interventions as needed (Foley and Faust 2010). Culling can also lead to abnormal social structures, with populations characterized by smaller family units with the age structure skewed towards younger individuals (Gobush et al. 2008; Slotow et al. 2008; Selier et al. 2014).

While poaching, whether for bushmeat or illegal wildlife trade, has many undesirable consequences, not least because it is unplanned, it is a form of lethal control and, as such, can provide information on potential consequences of culling. Gobush et al. (2008) studied the reproductive correlates of a disturbed social structure of an elephant population in Mikumi NP in Tanzania, and found that family groups exposed to poaching and trophy hunting in the past showed low group relatedness (i.e. a low number of first-order adult relatives) and weak social bonds. Females in groups displaying these characteristics were shown to have significantly higher faecal glucocorticoid levels, and, consequently, lower reproductive output (Gobush et al. 2008). Poaching in Ruaha NP led to lower group sizes and caused reproductive suppression (Mkuburo et al. 2020).

In a retrospective analysis of historical Kruger NP census information, Smit and Ferreira (2010) concluded that culling reduced the density of elephants along the major rivers. This effect eroded following the moratorium on culling (Smit and Ferreira 2010). Van Aarde et al. (1999) found that high-density elephant populations declined naturally without the need for culling, suggesting that density-dependent population dynamics alone may be enough to control elephant numbers (Robson and van Aarde 2018). Slotow et al. (2008) surmised that irruptive growth can persist for at least one generation, after which a new stable age structure will gradually establish itself; thus, the effects of culling could last for generations.

Goldenburg and Wittemyr (2017) found that orphans from poaching may experience decreased access to resources and reduced fitness in this matriarchal society. In a recent investigation, Parker et al. (2021) found that orphans had lower survival rates compared to non-orphaned age-mates, with population growth rates negatively correlated with orphaning probability and positively correlated with orphan survival. These results showed that adult elephant death, in addition to its direct effects, also indirectly decreases population growth through orphaning. These results demonstrate the detrimental impacts of orphaning on elephant survival and suggest that it should not be overlooked when quantifying the impacts of poaching. Similarly, Wittemyer et al. (2021) showed that elephant population growth was most sensitive to survival in young adults in the population. This suggests that enhanced parental care in elephants is key towards the attainment of high population growth, by increasing the probability of juvenile survival.

Unintended consequences of culling

When culling is implemented as a management approach, this may lead to the impression that regulators are encouraging the killing of elephants, leading to upsurges in killings of elephants by other people, potentially leading to crashes in elephant numbers (Fernando et al. 2008).

Here again we draw on the literature from studies of the consequences of elephant poaching, which provides insights into potential outcomes of culling. Like poaching, culling may lead to a breakdown in the social structure of elephants (Slotow et al. 2008). For example, poached elephant populations are characterized by smaller family units with a disproportionately high proportion of calves (Gobush et al. 2008). Also, poached populations often aggregate into large groups due to coalescing of family units, perhaps as a collective defence mechanism (Nyakaana et al. 2001). The indirect effect of this increase in group size is accelerated habitat degradation. Also, the death of matriarchs due to poaching causes disarray among family units, affecting a younger herd's ability to respond to threatening situations such as predation (McComb et al. 2011; Shannon et al. 2013) or drought (Foley et al. 2008).

Poaching also reduces heterozygous alleles, leaving the population susceptible to inbreeding depression (Gobush et al. 2009). Genetic effects of poaching on a large scale in Gorongosa NP led to large scale tusklessness (Campbell-Staton et al. 2021). Logically, intentionally removing entire groups through culling will remove the genetic material of that matriline from the population.

In a comparative study of elephant populations in Amboseli NP (Kenya) and Pilanesberg NP (South Africa), Shannon et al. (2013) found that elephants that experienced separation from family members when young (Pilanesberg) exhibited poor social knowledge, as they failed to distinguish calls from elephants they were familiar with from those they were not (Shannon et al. 2013). Furthermore, they were unable to separate calls from individuals of high social standing from those of low standing (Shannon et al. 2013). Thus, important decision-making abilities are impaired in elephants exposed to poaching, culling (the latter only in SA and not in Kenya) and translocation (Shannon et al. 2013). These elephants may also be affected by loss of cultural information and population-level experience (McComb et al. 2001).

There may be unintended consequences of culling on tourism. For example, a study of tourist and resident perspectives in the Associated Private Nature Reserves, adjacent to Kruger NP, found that tourists preferred non-intrusive interventions (Edge et al. 2017). Similarly, a social media sentiment analysis found a high negative sentiment towards trophy hunting and culling of elephants (Hammond et al. 2022).

Interventions such as culling that increase stress in elephants may result in elephants changing their patterns of spatial use, for example, moving away from prime tourism areas and retreating to refugia (Jachowski et al. 2012), or moving faster through corridors (Jachowski et al. 2013a). In response to poaching, both male and, more so, female elephants moved more at night than during the day (Ihwagi et al. 2018). Refuge areas tend to be those that are less frequented by people, and, hence, not prime tourist areas (R. Slotow, *pers. obs.*). Chronic stress and subsequent refuge behaviour displayed by elephants following culling may lead to elephant aggression towards humans, although the link between the two is still unsubstantiated (Jachowski et al. 2013a). Furthermore, the refuge behaviour of elephants may reduce their tourism value and, thus, reduce the ecotourism potential of PAs for elephant enthusiasts.

Fencing

Fencing is used primarily to influence the ranging of elephants; the many different types and their effectiveness are reviewed in Grant et al. (2008), with elements updated in Slotow (2012). More generally, wildlife fences are constructed for a variety of reasons but mainly to control access (Hayward and Kerley 2009). The benefits of wildlife fencing include increased landscape productivity (by controlling the timing and duration of landscape use by herbivores); reduced conflicts between wildlife and humans; prevention of mixing between wildlife and livestock (which reduces the risk of disease spread and livestock depredation); exclusion of wildlife from particular areas that are sensitive to disturbance; reduced encroachment by humans and poaching for bushmeat and other wildlife products; and increased landscape heterogeneity, achieved by inducing differential temporal use of certain parts of the landscape (Hayward and Kerley 2009; Pekor et al. 2019). In SA, fencing is regarded as the most effective method for containing of elephant populations within certain ranges, and thus as an important component of their management (Grant et al. 2008; Slotow 2012). Fences influence the ranging of elephants and make their use of the landscape more heterogeneous (Slotow 2012).

Besides boundary fences, internal fences can also be erected to exclude elephants from sensitive areas of reserves. This could be either to protect infrastructure and people, for example around camps, or to protect important habitats and areas set aside for habitat rehabilitation (Slotow 2012). For example, exclosure fences have been used in Addo Elephant NP to create botanical reserves (Lombard et al. 2001), and to protect key areas of sand forest in Phinda Private GR and Tembe Elephant Park (both in SA) (Lagendijk et al. 2011), as well as in Amboseli NP, Kenya (Barnosky et al. 2015).

PAs in SA are required to have electrified perimeter fences meeting minimum standards to ensure that it is effective against elephants (DEAT 2008; Grant et al. 2008; Slotow 2012). Di Minin et al. (2021b) identified hotspots of elephant and lion (*Panthera leo*) conflict with humans and identified priority areas where fencing could potentially be used to mitigate such conflicts, taking account of the capital and maintenance costs of fencing. They concluded that it may be possible to reduce the use of fencing in some areas in southern Africa, including SA (Di Minin et al. 2021b). Fencing high-conflict areas could reduce human mortality, costs to communities (such as time spent on crop and/or livestock protection), and risks of infectious diseases (Di Minin et al. 2021b). Such approaches may also include not fencing areas, or leaving gaps in fences where HEC is lower (Di Minin et al. 2021b). It should be noted that the high capital and maintenance costs of fencing may not repay themselves in countries with lower levels of human–wildlife conflict (Di Minin et al. 2021b).

Demographic responses to fencing

Elephants exhibit a range of migratory patterns; populations may be sedentary, nomadic, or exhibit partial migration patterns (Purdon et al. 2018). The maintenance of landscape connectivity is key for allowing elephants to maintain their normal yearly ranging patterns (Ngene et al. 2009; Purdon et al. 2018). However, fences fragment landscapes and limit the mobility of elephants (Boone and Hobbs 2004). Shrader et al. (2010) found that fencing restricted elephant movement mostly in the wet season, when they are able to move widely across the landscape as their ranging patterns are less limited by water and forage availability. However, Owens and Owens (1993) noted that drought conditions also cause elephants to migrate. Thus the prevention of dispersal of individuals from populations may inhibit the natural processes that regulate population levels in response to resource availability (Grant et al. 2008). Consequently, populations may overuse the resources within the fenced area, leading to declines of other species and even local extinctions within the fenced area (Hayward and Kerley 2009). Conversely, fences may restrict the immigration of individuals into the population, leading to a collapse in gene flow between populations, and threatening the genetic processes critical to the maintenance of heterozygosity and evolution of such populations (Hayward and Kerley 2009). This exposes populations to all the problems associated with insularity and a small population size (e.g. demographic, genetic and environmental stochasticity, and, ultimately, the 'extinction vortex'), threatening the future prospects of such populations (Pekor et al. 2019).

Fencing may also threaten metapopulation level processes whereby local population extinction is offset by recolonization and gene flow maintains high levels of heterozygosity (Hayward and Kerley 2009). This would reduce the probability of persistence of isolated populations compared to connected ones, increasing the risk of extinction for isolated fenced populations, which is opposite to the intended functions of fencing. Nevertheless, this requires further investigation as, to our knowledge, there are no studies of the demographic responses of elephants to fencing *per se*.

Unintended consequences of fencing

In a large-scale study across a range of study sites, Loarie et al. (2009) demonstrated that fences cause elephants to bunch up against them, which may increase their local impact on vegetation. In smaller reserves, however, the opposite may occur because of the fence edge effect; at Pilanesberg NP, feeding intensity was lower close to the fence, and increased as elephants moved away from the fence (Vanak et al. 2010). This can have a major impact in smaller reserves: At Pilanesberg NP, 26 km in diameter (Vanak et al. 2010), the effect began 3.8 km from the boundary fence, potentially concentrating the impact of elephants on vegetation towards the centre of the PA.

Many species of wildlife have to move between different habitats at different times of the year in order to satisfy their nutritional requirements; thus, the confinement of herbivores to small sections of the broader landscapes can reduce the ecological carrying capacity (ECC) of the area, potentially leading to massive population declines and ultimately extirpation (Pekor et al. 2019).

Fences do not represent absolute barriers to megaherbivores such as elephants. Elephants are very good at breaking fences by snapping or pushing over poles, and even use their tusks to snap electrical wires (Grant et al. 2008; Slotow 2012). Poor fence maintenance, often due to shortage of funds or human resources, is a particular issue, as elephants first learn to break out through weak points, and then use their acquired skills to break through fully functional fences (Grant et al. 2008; Slotow 2012). Internal fences, which may be needed to protect lodges or other infrastructure, are often where the first incidences of fence-breaking occur (R. Slotow *pers. obs.*). Learned fence-breaking behaviour is difficult to correct, and the animal becomes a habitual fence-breaker, and may then need to be euthanized as a problem animal (Slotow et al. 2008). Fence-breaking necessitates repair, capturing of escaped animals, and may be costly in terms of subsequent incursions by problem elephants who raid crops in neighbouring communities, thus exacerbating HEC (Hayward and Kerley 2009). In some areas, use of two-strand electric fences that prevent elephants from entering, but allow other animals to do so, can be effective (Slotow 2012). However, this can have unintended consequences in that, in the absence of elephants, increasing meso-herbivore numbers can have cascading effects on other species (Lagendijk et al. 2011; 2012). As fencing confines elephants to small areas, they are unable to offset local food shortages by shifting their spatial distribution (Shrader et al. 2010). Consequently, their survival becomes more dependent on rainfall patterns, potentially leading to mass mortalities during periods of drought (Wato et al. 2016).

By preventing migratory movements, fencing can inhibit natural processes that regulate populations of species within bounds set by resource availability (ECC) (Hayward and Kerley 2009). This may result in over-use of an area, causing declines or extirpation within closed areas (Hayward and Kerley 2009). Erection of fences between communities and wildlife areas can cause conflict if proper consultation is not undertaken (Di Minin et al. 2021b). Moreover, fencing one area to mitigate HEC may transfer that conflict to another location (Osipova et al. 2018).

Range expansion

Fragmentation of ecosystems, especially due to fences, has reduced migrations, leading to population declines of migratory species (Bartlam-Brooks et al. 2011). Elephant ranges are rarely fully incorporated within PAs (Douglas-Hamilton et al. 2005; Graham et al. 2009); indeed, Thouless et al. (2016) suggest that only 30% of elephant ranges are within PAs. Thus, providing access to additional land is viewed as key to ensuring the long-term sustainability of elephant populations within areas enclosed by fences, by reducing their relative density and, therefore, their impact on ecosystems (van Aarde and Jackson 2007). Besides increasing the area of the reserve, a second objective of range expansion that relates specifically to the management of elephants in the SA context is the removal of bottleneck areas, and sharp angles into which animals may be directed as they move along the fence, increasing the risk of breakouts in these areas (R. Slotow, *pers. obs.*). While many reserves have increased elephant range areas by incorporating neighbouring areas, or straightened fence lines to reduce bottlenecks and breakouts (Druce et al. 2008; R. Slotow, *pers. obs.*), this has not been well documented in the literature. The largest incorporation of areas into a fenced reserve occurred in the Greater Kruger ecosystem, where adjacent private reserves were incorporated into the NP by shifting the boundary fence westward (Grant et al. 2008; R. Slotow unpublished data). This range expansion was further increased through the removal of the eastern boundary fence along the international boundary, connecting Kruger NP to Limpopo NP in Mozambique.

Demographic responses to range expansion

The human alteration of the global environment has led to significant reduction in the amount of habitat available to elephants and has simultaneously curtailed their migratory movements (Purdon et al. 2018). This has made the provision of access to additional land a key aspect of conservation strategies. By reconnecting habitats, it is possible to re-establish past migratory routes of species, once physical barriers are removed, and to augment local populations (e.g. Bartlam-Brooks et al. 2011). Nevertheless, there is currently no published literature, to our knowledge, on the demographic responses of elephants to range expansion, pointing to the need for more studies.

Unintended consequences of range expansion

Dropping of fences has expanded the range available to elephants; however, there is little published literature on the subject (Druce et al. 2008). Druce et al. (2008) studied the response of elephants to fence removal between Phinda Private GR, SA and two neighbouring communal reserves. After fence removal, older, recently introduced bulls responded quickly and moved into a new area, whereas young bulls and family groups took a long time to do so (Druce et al. 2008). However, more than a year after fence removal, most elephants had only expanded their ranges slightly into the new area. While this may have been because they were not under strong pressure to do so (Druce et al. 2008), these observations suggest that elephants are cautious about exploring new areas moving into them over a long time (Druce et al. 2008). Bulls are more tolerant of low-quality diets and are exposed to less risk by exploring unknown ranges (Druce et al. 2008; Woolley et al. 2009).

Thus, before fences are removed, the movement ranges of elephant groups in the area should be taken into consideration. For example, opening up fences for sedentary populations may lead to mixed results, as groups may be unlikely to incorporate new areas into their ranges. However, they may do so if population density is very high, or if the new area contains features that are attractive to elephants, such as water points, rivers, or preferred habitat or tree species, as has been observed in areas incorporated to the west of Kruger NP (R. Slotow, *pers. obs.*). There are also other challenges, for example, elephants may move into a new area of the reserve that is not set up for tourism, or further from established lodges (R. Slotow, *pers. obs.*). Furthermore, elephants moving into new areas that previously had no resident elephants may selectively feed on at-risk species of trees, rapidly reducing their abundance in these areas (O’Connor and Page 2014; O’Connor 2017). In addition, when new areas include a large river, elephants may spend a substantial amount of time there, impacting on high-value riverine vegetation (R. Slotow, *pers. obs.*). All these effects require further investigation, so that plans can be made for future mitigation measures.

Corridors

Elephants are wide-ranging species, with distinct wet and dry season ranges (Ngene et al. 2010; Kaszta et al. 2021). When moving between these seasonal ranges, elephants use corridors (Douglas-Hamilton et al. 2005; Ngene et al. 2010). Increasing connectivity between elephant ranges is seen as one way to reduce the impacts of elephants in areas where they have become over-abundant, as well as being a strategy to stabilize regional elephant populations (Douglas-Hamilton et al. 2005; Roever et al. 2013; Green et al. 2018). At an individual level, corridors allow elephants to meet their nutritional requirements by providing access to key resources which are otherwise scarce in space and/or time (Ngene et al. 2010). At a population level, corridors allow elephants to respond to stochastic events such as drought or threats such as poaching, via dispersal or migration (Shrader et al. 2010).

Moreover, corridors allow elephants to exist as a metapopulation, reducing the minimum size of each subpopulation necessary to be viable through the genetic and demographic contributions of immigrants (Graham et al. 2009). A land-use planning study across northern Kwazulu-Natal, SA, demonstrated the potential importance of elephant corridors (Di Minin et al. 2013). Corridors can also serve to increase connectivity for other wildlife, as elephant occurrence (both inside and outside PAs) is strongly associated with that of other large mammals (i.e. ungulates and large carnivores) (Crego et al. 2021). Furthermore, elephant corridors benefit communities surrounding elephant ranges by reducing HEC and increasing tourism revenue (Osborn and Parker 2003). Lastly, corridors can allow elephants to adapt to climate change by providing access to suitable habitat areas (Zacarias and Loyola 2018).

As elephants show differential use of habitat across space, the existence of movement corridors has been demonstrated both between (Douglas-Hamilton et al. 2005) and within PAs (Jachowski et al. 2013a). However, elephant distribution across landscapes is likely determined by a trade-off between human disturbance and forage availability (Graham et al. 2009). When moving through human-dominated landscapes, elephants experience a range of negative effects, such as reduced foraging and resting time, increased agitation (Kumar and Singh 2011), and even mortality. Elephants use avoidance tactics to reduce contact with people; these include: reducing movements in areas close to human settlements; moving through human-dominated landscapes at night; increasing the speed of transit in areas close to human development; and completely abandoning areas when human densities reach a certain threshold (Blake et al. 2008; Graham et al. 2009; Ngene et al. 2010; Jachowski et al. 2013a). In particular, roads and highways may serve as a barrier to elephant movement (Green et al. 2018, but see Okita-Ouma et al. 2021 for a different view), although elephants may use habitats near secondary roads, especially if these roads are located closer to water sources, when human disturbance is low at night, or when the vegetation on road edges is of higher quality than in areas far from roads (Green et al. 2018). In order to maintain the integrity of elephant movement across landscapes, future human development within areas identified as elephant corridors should be avoided, and instead located in areas that are less important for habitat connectivity (Ngene et al. 2010). In 2017, when the new Mombasa–Nairobi railway was built between the Tsavo East and Tsavo West NPs, insufficient mega-fauna passages and underpasses were constructed for elephants to compensate for restrictions on movements between ancestral ranges caused by the presence of the railway (Okita-Ouma et al. 2016, 2021).

Demographic responses to corridors

Van Aarde and Jackson (2007) proposed adoption of a metapopulation approach towards elephant management. However, the metapopulation as a whole remains stable, because immigrants from one population are likely to re-colonize habitat left open by the extinction of another (Pulliam 1988). Moreover, individuals may also emigrate from a large to a small population, thereby rescuing the small population from extinction ('rescue effect') (Brown and Kodric-Brown 1977). Managing elephants using this approach depends on the linkages provided by corridors to allow the dispersal of individuals among populations (Douglas-Hamilton et al. 2005). Despite the interest in the metapopulation approach, and widespread acceptance of the importance of elephant corridors in general, we are not aware of any study on the demographic responses of elephants to movement corridors. Nevertheless, since corridors increase the overall amount of habitat available to elephants (Ngene et al. 2010; Roever et al. 2013; Adams et al. 2017), and also reduce their susceptibility to stochastic events (Shrader et al. 2010), the presence of elephant corridors may be expected to lead to an increase in elephant population numbers regionally, as well as enhancing genetic processes (gene flow, heterozygosity etc.), thereby reducing the requirement for translocation of elephants for genetic management . Both of these elements should be prioritized for further investigation.

Unintended consequences of elephant corridors

A risk associated with elephant corridors is that elephants can move into surrounding human settlements, causing damage to crops and endangering human life, thereby exacerbating HEC (Kikoti et al. 2010). For example, Kikoti et al. (2010) found that two villages bordering an elephant corridor connecting Kilimanjaro NP (Tanzania) to the Amboseli NP (Kenya) experienced increased rates of crop-raiding by elephants. This problem was particularly acute during the wet season, which is the main crop-growing season in the region (Kikoti et al. 2010). Secondly, elephants moving through corridors, which are unsafe areas from their perspective, exhibit elevated stress levels which may lead to aggressive behaviours, increasing HEC in human settlements bordering corridor areas, or in corridor areas within reserves themselves (Jachowski et al. 2013a; Ahlering et al. 2013; Tingvold et al. 2013; Hunninck et al. 2017). High levels of HEC may lead to negative attitudes towards conservation among members of surrounding villages, and even elephant deaths as a result of retaliatory killings (Kikoti et al. 2010; Selier et al. 2016).

However, corridors are still used by elephants when their stress levels are elevated (Jachowski et al. 2013a). Elephants move faster through corridors than in PAs and display reduced tortuosity of movement (Douglas-Hamilton et al. 2005; Ngene et al. 2010; Jachowski et al., 2013a). (There is no set width or length for corridors. They are areas through which elephants move between two core areas and vary according to the local situation. Neither is there a specific design for them (R. Slotow, *pers. obs.*). Thus, although corridors expose elephants to high levels of stress, this is unlikely to compromize their ability to connect disparate populations, or refuge areas within reserves. Furthermore, Munshi-South et al. (2008) found that elephants in a corridor which was being subjected to oil exploration in Gabon did not show an elevated stress hormone response, as the management of the oil concession had made efforts to minimize stressful interactions between humans and elephants. This suggests that if disturbance from humans is limited and their lives are not threatened, elephants adapt to living with humans, without elevated stress levels and associated HEC (Munshi-South et al. 2008). A specific unintended consequence of corridors between refuge areas within reserves is an increased risk of HEC, if people are not aware that they are in an elephant corridor and simply it as part of the larger PA (Jachowski et al. 2013a). In these cases, consideration should be given to signage and raising awareness among visitors to reduce the risk of HEC.

A further consideration is that corridor presence does not mean use, leading to a potential mismatch between corridor use and corridor function (Horskins et al. 2006), whereby the effort made to protect the corridor may not achieve the intended outcome. For example, Green et al. (2018) found that only 50% of elephants that entered the Mount Kenya Elephant Corridor in Kenya traversed its entire length, with many coming back to the same entry point they used, and others taking much longer than envisaged to move through the corridor. Studies also report differential use of corridor areas by elephants (Gangadharan et al. 2017; Green et al. 2018; Osipova et al. 2019), suggesting that elephants use some parts of corridor areas simply as an extension of habitat, and other parts for transit (Green et al. 2018; Williams et al. 2018). Generally, elephants were found to spend more time in areas with extensive woody cover and low human disturbance levels, while using the more open parts of the corridor for transit (Green et al. 2018). Heavily utilized areas may be more subjected to habitat degradation, undermining the role of corridors in reducing elephant impact on vegetation (Green et al. 2018). However, the primary purpose of setting aside corridors is to provide an identified passage through which elephants move between protected areas that avoids human settlements, thereby reducing HEC (Kikoti et al. 2010).

Moreover, corridors may only exist on paper (similarly to 'paper parks') if measures to protect them from human development are not put in place (Midha et al. 2018; Schussler et al. 2018). If elephant corridors are identified, but left unprotected, inevitably development will occur, undermining their effectiveness (Schussler et al. 2018). Fortunately, elephants are long-living species, with genetic differentiation of populations taking a long time to occur (Lobora et al. 2018). This suggests that the effects of isolation on elephant populations will take time to manifest, buying crucial time for conservationists to create elephant corridors, or to use other management approaches to avert habitat fragmentation and consequent isolation of elephant populations.

Artificial water provision

Surface water distribution is one of the most important factors, if not the prime factor, affecting the distribution of elephants across landscapes (Chamaille-Jammes et al. 2007a; Smit et al. 2007a, 2007b; Ngene et al. 2009). Thus, the availability and distribution of surface water affects the impacts of elephants on vegetation (Fullham and Child 2013). Provision of artificial water supply causes high local elephant densities; thus, water supply management is an important tool for managing elephant density and distribution (Chamaille-Jammes et al. 2007a). In Kruger NP, it was hypothesized that the removal of artificial water supply would reduce elephant impacts on the system, primarily through increasing the heterogeneity of their habitat use (Owen-Smith et al. 2006; Smit et al. 2007a; Purdon and van Aarde 2017). However, in PAs, particularly smaller ones, artificial water points may represent the main sources of water, and artificial water sources are often installed in front of tourist lodges to attract elephants and other wildlife (R. Slotow, *pers. obs.*). Moreover, the effects of water manipulation are likely to be dependent upon context, especially reserve size and management objectives (Smit et al. 2007a).

Closure of artificial water points away from rivers may not reduce elephant numbers, and could, consequently, result in negative impacts on the vegetation and biodiversity if elephants concentrate along rivers (Chamaille-Jammes et al. 2007a). Provision of artificial water sources may increase elephant numbers where surface water is limited or non-existent in the dry season, suggesting that reduction of some artificial water point is going to be effective mostly as a means of controlling elephants numbers in areas where population numbers are severely limited by water availability (Chamaille-Jammes et al. 2007). Furthermore, most elephant control measures assume that elephant numbers are above the ECC of reserves. If populations do not decline following water point closure, this suggests that the elephant population has yet to reach ECC, i.e. levels where resource availability starts to have a noticeable effect on demography (Chamaille-Jammes et al. 2007a).

Demographic responses of artificial water provision

Elephants are water-dependent species, requiring access to water every two to three days (Smit et al. 2007a, 2007b). Consequently, their distribution and abundance across landscapes are determined by surface water availability (Smit et al. 2007a, 2007b; Ngene et al. 2009). There is a large body of literature showing that artificial water provisioning leads to a significant increase in elephant numbers at a local level, especially in areas where water is limited or non-existent in the dry season (Chamaille-Jammes et al, 2007a, 2007b; Smit et al. 2007a, 2007b; Smit and Ferreira 2010). However, Chamaille-Jammes et al. (2007b) reported the relationship between surface water density and elephant densities reached an asymptote at densities of 3 individuals/km2. They suggested that, at densities above this threshold, food availability becomes the principal limiting factor for elephant densities (Chamaille-Jammes et al. 2007b). A corollary to this would be that the removal of artificial water points would reduce elephant numbers in areas where they are over-abundant (Smit et al. 2007a; 2007b), but this does not appear to be the case (Chamaille-Jammes et al. 2007a; Franz et al. 2010; Robson and van Aarde 2018).

Elephants not only use water for drinking, but also for thermoregulation, and change their speed of movement towards and away from water at high temperatures (Thaker et al. 2019). Providing artificial water points decreases the distance elephants have to travel to access water, which may reduce stress levels and, potentially, mortality among young elephants in times of drought (Woolley et al. 2008a). Additional research on this is required, especially given the potential increase in temperatures and heat stress due to climate change (Ncongwane et al. 2021).

Unintended consequences of artificial water provision

The presence of artificial water points causes intense and localized impact on vegetation close to water, leading to a piosphere effect (heightened impact on vegetation close to the water point) (Kerley et al. 2008), which is more intense around artificial than natural water sources (Chamaille-Jammes et al. 2009). Along a 60–km transect in Chobe NP, Botswana, there was a piosphere effect at the local scale, with vegetation impact decreasing with distance from water, but at the larger landscape scale this piosphere effect disappeared (Fullman and Child 2013). There was a strong piosphere effect of elephant impact on succulent thicket vegetation in Addo Elephant NP, SA, close to water (Landman et al. 2012). Researchers advised against the establishment of artificial water points in the thicket habitat because of this. Piosphere effects may only emerge over a long period, and there may not have been enough time for such effects to become manifest in some smaller reserves and PAs where elephants have been reintroduced (Kerley et al. 2008). Nevertheless, vegetation utilization gradients by elephants in areas close to water points is a controversial conservation issue (Smit et al. 2007a, 2007b, 2007c; Chamaille-Jammes et al. 2007b). This is because savannah ecosystems are complex, and it is not easy to separate the effects of elephant impacts from those of fire management, disease, rainfall, soil mineral content, grazing by other herbivores, human activities, etc. (Shannon et al. 2008; Vanak et al. 2012; Guldemond et al. 2017). For example, the proportion of large trees that were utilized and pushed over in southern Kruger NP increased with distance from permanent water, and this effect would be heightened by artificial water provision (Shannon et al. 2008).

Hayward and Zawazdka (2010) showed that elephants generally exert more influence than rainfall on vegetation condition, although in some studies both elephants and rainfall combined to drive vegetation dynamics. Contrastingly, among the factors considered in a study by Guldemond et al. (2017) (elephant numbers, study duration, rainfall, tree cover, primary productivity, and presence of artificial water points), only primary productivity was found to influence elephant impacts on vegetation. This suggests that elephant impacts may be site-specific, and that applying uniform management measures across sites with varying environmental conditions may be inappropriate. Therefore, tailor-made solutions are required. Most studies on elephant impacts have focused on individual sites, with limited replication, lack of suitable controls, and incorrectly assigned response variables, leading to contradictory results (Hayward and Zawazdka 2010; Guldemond et al. 2017). While there is some understanding of local piosphere effects, further research is needed on spatial and temporal scaling in relation to piospheres, as well as their influence on the broader landscape.

An aspect to take into consideration with regards to potential unintended consequences of artificial water point provision is that it not only affects elephants, but also other herbivores, especially water-dependent species (De Beer and van Aarde 2008). For example, at high densities, elephants monopolize water resources while they are using them, leading to marked temporal partitioning in water point use between elephants and other species (Valeix et al. 2007). Sutherland et al. (2018) however, indicated a weak, positive effect of elephants on other species. This may disrupt the time investment of other species, leaving less time available for engaging in fitness-enhancing activities (Valeix et al. 2007). Furthermore, increased elephant densities may have cascading effects on other species by causing shifts in herbivore community structure. For example, in three protected areas in Namibia, the biomass of grazers increased more than browsers with increased density of elephants due to artificial water provisioning, shifting the community towards one dominated by grazers, particularly mega-grazers (white rhinoceros *Ceratotherium simum*, African buffalo *Syncerus caffer*, and hippo *Hippopotamus amphibius*) (De Beer and van Aarde 2008).

Fire management

Prescribed burning (fire management) is widely used especially with southern Africa, as an intervention to increase grazing quality, or to prevent or reduce woody plant encroachment (Bond and Archibald 2003). Fires are intentionally started by managers to achieve specific aims, and different approaches have been used over time, from burning grasslands after a set time, towards a more natural approach to simulate natural fire return periods (van Wilgen et al. 2003). We are not aware of any NPs or PAs that currently implement burning for the specific purpose of providing additional food resources to elephants. Nevertheless, there is a large literature of the relative effects of elephants and fire on savannah vegetation (Smit and Prins 2016). Elephant herbivory and fire are major drivers of vegetation and biodiversity dynamics in savannah, with elephant herbivory considered the predominant driver of large tree dynamics, and fire being secondary (Vanak et al. 2012; Morrison et al. 2016).

These drivers, however, interact with each other in complex ways (Shannon et al. 2011; Vanak et al. 2012; Pellegrini et al. 2017). The probability of mortality of the ten most common tree species in the study area in Kruger NP depended not only on the type and intensity of elephant-induced damage and fire, but also on the historical sequence of damage by these agents, extending over 12 years (Das et al. 2021). Fire increases the incidence of elephant damage to trees by increasing the frequency and intensity of herbivory due to vegetative regrowth following fire (Pringle et al. 2015). On the other hand, elephant grazing and browsing affect fuel loads, leading to changes in fire intensity (Pringle et al. 2015; Morrison et al. 2016). Fire also affects herbivore spatial distribution at various scales. For example, elephants tend to be found more frequently in areas recently subjected to burns as there is a more vegetative regrowth (Shannon et al. 2011; Pringle et al. 2015). Despite the interactions between fire and herbivory, it is hard to separate the effect of elephants from those of other herbivores, and the effects of fire, soil, and rainfall (Smit and Prins 2016).

Demographic responses to fire management

The only paper we are aware of that considers the demographic effects of fire on elephants is that of Woolley et al. (2008b). This documents an unusual event, when a large portion of Pilanesberg NP was consumed by fires over a short period, and herds of elephants were caught up in the fires, with some dying and others being severely injured (Woolley et al. 2008b). Severely affected breeding herds reduced daily displacement, with increased daily variability; reduced home range size; spent more time in non-tourist areas; and associated less with other herds (Woolley et al. 2008b). Most mortality occurred in the juvenile age class, causing a change in post-fire population age structure (Woolley et al. 2008b).

Unintended consequences of fire management

After the Pilanesberg NP fire, there was a strong flight response, with elephants that were injured moving into non-tourist areas (Woolley et al. 2008b). As discussed above, such refuge behaviour may lead to aggressive encounters with humans and extensive habitat degradation in the refuge areas (Jachowski et al. 2012). A possible unintended consequence of high elephant densities in interaction with fire is high levels of tree death, which has the potential to transform savannah ecosystems from a closed to an open shrubby vegetation (Shannon et al. 2011). For example, by ringbarking trees, elephants make trees more susceptible to damage by fire, especially by exposing the xylem to intense heat, and subsequent damage, leading to reduced water conductivity in the stem, resulting in high stem mortality (Moncrief et al. 2008; Holdo et al. 2009). The impact of subsequent fire was higher on trees previously browsed by elephants than on undamaged trees (Shannon et al. 2011). Thus, the sequence of fire and elephant damage, and interval between them, are important (Das et al. 2022).

Consequences of elephant management on tourism

The burgeoning southern African elephant population, and the intervention strategies to deal with it, is one of the most hotly debated and emotionally charged contemporary conservation issues (Owen-Smith et al. 2006; Dickson and Adams 2009). Edge et al. (2017) found that visitors to PAs reported a high level of attraction to vegetation not impacted by elephants, and considered impacted habitat to be less attractive. This suggests that the impacts of elephants may affect the aesthetics of vegetation, with consequences for visitor attractiveness and, consequently, tourism potential of PAs. In contrast, Arbieu et al. (2017) found that tourist experiences in PAs decline in areas with high vegetation density, with a positive relationship between mammal densities and tourists' experiences. In particular, tourists showed a dislike for areas with high vegetation density (Arbieu et al. 2017). Moreover, it became harder to spot mammals above certain thresholds of vegetation density, especially where mammal densities were low. Arbieu et al. (2017) concluded that the openness of grass-dominated savannah ecosystems provided excellent wildlife viewing opportunities, with tourist satisfaction linked to their wildlife viewing success. Similarly, Gray and Bond (2013) found that herd sizes, densities and, therefore visibility of animals in PAs were reduced in densely wooded areas, due to reduced habitat heterogeneity and possibly as a predation risk avoidance strategy. Visitor satisfaction declined with reduced visibility of wildlife (Gray and Bond, 2013). Other studies found higher density and richness of mammalian herbivores in areas with more grass cover relative to shrub cover, with herbivores distributed largely in open areas (Gandiwa 2014; Soto-Shoender et al. 2018). Combined, these results suggest that elephant impacts on vegetation may positively affect visitor satisfaction by increasing vegetation openness, leading to improved wildlife viewing experiences, and creating a more aesthetically pleasing environment than densely wooded areas (Gray and Bond 2013). Areas of high aesthetic value to tourists, such as along riverine areas, may be compromized by fencing (Slotow 2012).

Tourists prefer indirect forms of elephant management, whereas local residents prefer more direct methods of culling and translocation, but not contraception (Edge et al. 2017). Similarly, people from non-range States evinced highly negative sentiments to trophy hunting and culling of elephants, whereas people from range States were more concerned about HEC, poaching, and promoting elephant tourism (Hammond et al. 2022). As international tourists generally contribute more than domestic tourists towards tourism revenues in African PAs (Lindsey et al. 2007), the implications of these results are that intrusive elephant management approaches are more likely to reduce tourism revenues than non-intrusive ones (Edge et al., 2017). In addition, some interventions increase stress in elephants, leading them to change their spatial use of habitats, generally by retreating to refugia (Jachowski et al. 2012) away from prime tourist areas reducing the opportunity to view elephants (R. Slotow, *pers. obs.*). The corollary is that areas free of tourists play an important role by providing elephants with opportunities to reduce their stress levels.

Studies have demonstrated that tourism may have a direct negative effect on elephants (Pretorius 2003; Burke et al. 2004). For example, elephant stress hormones are higher in areas with game drives, and stress levels reach a peak while the game drives are taking place (Pretorius 2003). Moreover, if tourist vehicles come too close to elephants, or if there are too many vehicles, elephants display behaviours associated with risk avoidance and stress (e.g. bunching, moving further away, moving to thick vegetation, and moving to safe areas away from tourists) (Pretorius 2003; Burke 2004). In addition, Szott et al. (2019a, 2019b) found that as tourist pressure increased, elephant aggression towards conspecifics increased, especially by male elephants. Furthermore, they found that elephant herds were increasingly likely to move away when more vehicles were present. As tourism activities and vehicle presence increased, elephants altered their behaviour from feeding to fearful, alert, stress-related or aggressive behaviours (Szott et al. 2019a). Thus, although tourism viewing experiences are important for revenue generation, tourists themselves negatively affect future sightings of elephants for others, reducing future tourism potential.

Overall, these results suggest that managers of areas where elephants are present should train staff (e.g. guides) to monitor elephant behaviour to identify potential negative effects of tourism pressure on elephant welfare, as well as ensuring that tourists/ tourist vehicles maintain the minimum distances from elephants required to meet high standards both for elephant welfare and tourist safety (Szott et al. 2019a; 2019b). The closure of artificial water points is likely to have negative impacts on the tourism potential of PAs by restricting elephant movement to areas with high natural water availability (e.g. Smit et al. 2007a, 2007b), but this important issue is yet to be investigated.

Discussion

A range of interventions has been implemented to reduce elephant numbers, population growth rates, density, or movement in regions where they are, or potentially could become locally over-abundant, or to contribute to conservation goals. These interventions include contraception, vasectomy, translocation, hunting, culling, fencing, range expansion, connectivity, water provision, and fire management (Owen-Smith et al. 2006; van Aarde and Jackson 2007; Scholes and Mennell 2008). In this study, we conducted a systematic literature review to update our understanding of these interventions in the 2008 assessment by Scholes and Mennell (2008), including demographic responses to the interventions their unintended consequences, and interactions with tourism. Interventions that are effective in achieving intended outcomes may also be associated with a range of unintended consequences. We found large disparities between the amounts of research effort directed towards the different approaches, with, overall, very few studies that explicitly investigated their unintended consequences.

In general, the research published since 2007 has contributed to increased understanding of the effectiveness of the various interventions. It should be borne in mind that we only reviewed papers dealing with elephants, and there has been substantial other work published on some of the indirect management interventions, such as water provisioning, fire management, corridors etc. However, it should be noted that, in addition to assessing the method in the context of elephants, we also examined it effects on elephants, especially on their ranging and on elephant population demographics.

We found that there is minimal information available on the demographic effects of indirect interventions (such as fire management, fencing, range expansion, and corridors) on elephants, or on how they affect local spatial use by elephants. However, there is a good body of literature on the demographic and spatial effects of water point provisioning and closure of water points. Water provisioning increases numbers locally, reduces mortality, for example from drought, and may increase population growth rates (Chamaille-Jammes et al. 2007a, 2007b; Smit et al. 2007a, 2007b; Smit and Ferreira 2010), as well as greatly influencing spatial use by elephants (Chamaille-Jammes et al. 2007a; Smit et al. 2007a; 2007b; Ngene et al. 2009). Conversely, closure of water points can reduce growth rates, and increase heterogeneity in spatial use and impacts (Owen-Smith et al. 2006; Smit et al. 2007a; Purdon and van Aarde 2017). Water provisioning is, therefore, the most effective indirect intervention if the aim is to influence elephant spatial use and increase population growth rates; however, it is not clear that closure of water points leads to a reduction in population (Chamaille-Jammes et al. 2007a; Franz et al. 2010; Robson and van Aarde 2018). It should be noted that severe droughts can cause mortality even when water is available, as food near water may be depleted; however, there would need to be very high mortality of infants and just weaned calves (85% mortality of calves at least every eight years) for this to lead to a persistent decline in population size (Woolley et al. 2008a).

Excluding elephants from potential high-conflict areas using fences is effective in mitigating risks associated with HEC (Di Minin et al. 2021b). These are not necessarily conceptualized as continuous barriers around PAs in the traditional sense, but rather target the immediate area of conflict, using a risk assessment approach (Di Minin et al. 2021b). Innovations in approaches to fencing under such circumstances are necessary, such as the recent work of La Grange et al. (2022), who tested a soft virtual boundary, placing deterrent scents along habitual pathways of elephants from natural areas to croplands, thereby deterring them from leaving their daytime refugia. While Di Minin et al. (2021b) factored in the capital and maintenance costs of fencing in their economic analysis of where to consider fencing, the high costs of fence maintenance are challenging at a time of declining conservation budgets (Grant et al. 2008). Additional research is needed on approaches to fencing for specific purposes (Slotow 2012), including non-continuous fencing to allow natural movement of elephants across broader landscapes. In general, work on HEC, or human–elephant co-existence (HECx), in the unfenced landscapes that characterize many elephant ranges across Africa has long been a focus of research (Hoare 2015). The different elements of HECx were reviewed by Shaffer et al. (2019), who also emphasize the need to apply ecological, anthropological, and geographical knowledge and tools for long-term sustainable solutions. In their review of HECx, Gross et al. (2022) identify six strategic areas that need to be considered, one being technical, which covers the types of interventions we have reviewed here. Others address monitoring, legislative, social, spatial management, and financial issues. Van de Water et al. (2022a) set out the TUSKER framework for more sustainable people–nature interactions in the context of elephant conservation, emphasizing the need to balance integrity of nature with social cohesion and human well-being, as well as moderating the use of nature in accordance with widely accepted values, aspirations and rights. Such holistic approaches address conflicts arising from interactions with many animals, as opposed to the targeted management of habitual crop raiders (Hahn et al. 2022) reviewed here under the culling section. Clearly, more research is needed on the demographic and spatial effects of some of the indirect interventions, to gain a better understanding of elephant behaviour under different circumstances.

Among direct interventions, there has been substantial work on the various forms of contraception, such that these methodologies are becoming refined and well understood. The impact of direct interventions on demography and spatial use is well understood. In this context, further research on their technical aspects is less important than addressing the urgent need to better understand the impacts of indirect interventions, as indicated above.

Importantly, this review identified a range of unintended and undesirable consequences of the interventions, but, again, there has been more research on some of these than others. Although the provision of access to additional habitat for elephants is a key management approach to reduce the local impacts of elephants on the environment, this aspect has received only scant research attention. Of particular concern is the increase in HEC in communities surrounding corridor areas which can lead to the development of negative attitudes towards conservation among community members (e.g. Kikoti et al. 2010). An unintended consequence of fire management occurs when fire combines with damage caused by elephants increase tree mortality (Shannon et al. 2011, Vanak et al. 2012, Das et al. 2022). The potential unintended consequence of fire killing trees that were previously damaged by elephants needs to be considered in further studies.

Although translocation is an important part of elephant management approaches, few studies have assessed its unintended consequences. In addition, very few studies have conducted long-term post-release monitoring of the translocated elephants, which means that little is known about the success or otherwise of this approach.

In addition to its controversial nature, as well as its ineffectiveness (in the long term) in reducing elephant numbers, culling is the elephant management approach associated with the highest number of unintended consequences. More clarity is required on the fact that trophy hunting is primarily for economic benefit, and that selective removal of adult males is ineffective in reducing population size except in very small populations.

Importantly, this review also assessed perceptions of tourism and the potential impact of tourism on elephants. Elephant impacts on habitat may alter the sense of place (Hausmann et al. 2016), as will some management interventions, including provision of water which creates artificial landscape effects through piospheres (Kerley et al. 2008). Conversely, provision of water attracts animals in general, making them more accessible and visible to tourists (Sutherland et al. 2018). There may be interactions between management interventions and tourism satisfaction, which require further investigation. Tourists prefer non-lethal interventionist approaches (Edge et al. 2017), and the potential negative effect of resuming mass culling on ecotourism revenues has not been investigated. Harvey (2020) estimated the potential cost of reputation damage from the captive lion industry in South Africa to be USD 2.79 billion, and a similar risk would need to be considered in decisions around mass culling of elephants.

Different aspects of elephant management can evoke different reactions from people in general, and specifically from tourists, and more research is needed to understand these important dynamics. Social media analysis provides an opportunity to collect data from a range of people, although it does exclude those without internet access (Hausmann et al. 2020). The word elephant appears frequently in tourist social media, and the sentiment associated with seeing them can be interpreted; for example, in Addo Elephant NP, joy is associated with elephants (Haussmann et al.

2020). Management interventions such as trophy hunting and culling evoke the strongest negative sentiment among potential tourists from non-range states, while people in range States have positive sentiment towards promoting tourism (Hammond et al. 2022). People from non-range States were more concerned than those within range States about elephant welfare issues (Hammond et al. 2022). Given its importance in supporting elephant conservation on the ground (Naidoo et al. 2016), more research is required on the potential effects of elephant management on tourism.

The results make clear that the 'elephant problem' brings to the fore the issue of equilibrium versus non-equilibrium control of ecosystem dynamics. In the 'equilibrium' school of thought, density-dependent population regulation factors are prime determinants of animal population size (Sinclair and Krebs 2002). Based on a perspective of ecosystems dominated by equilibrium dynamics, high densities of elephants and the resultant habitat change are perceived as an undesirable disruption of equilibrium conditions (Gillson and Lindsay 2003). This perspective is associated with a 'command and control' management style (e.g. culling, translocation, contraception, etc.) that aims to maintain animal numbers at levels compatible with the steady state (Gillson and Lindsay 2003; Owen-Smith et al. 2006; Guldemond and van Aarde 2008).

The 'non-equilibrium' school of thought, on the other hand, predicts that plant composition and biomass are primarily driven by rainfall rather than by grazing/browsing pressure (Vetter 2005). Thus, animal numbers are maintained at low densities by frequent droughts and have little impact on vegetation change (Ellis and Swift 1988; Illius and O'Connor 1999). From this perspective, variability in rainfall is an important driver of ecosystem dynamics and determines the spatial and temporal heterogeneity required for ecosystem diversity, stability, and resilience (McNaughton et al. 1988). This perspective is associated with a "laissez-faire" (i.e. non-intervention) management style (van Aarde and Jackson 2007; Guldemond and van Aarde 2008).

Nevertheless, elephant management approaches are becoming more centred on promoting ecological processes to regulate elephant numbers naturally (Owen-Smith et al. 2006; van Aarde and Jackson 2007; Ferreira et al. 2013). Clearly, such an approach requires areas large enough for natural processes to play out; the issues of reserve size and the need for management interventions to control elephants or their impact are poorly understood, and remain a priority for future research (Kerley et al. 2008; Delsink et al. 2013). In addition, increased consideration is being given to inclusion of broader social and economic elements into decision-making, emphasizing the need to reduce disservices such as HEC, and achieve a better balance between the integrity of nature and social cohesion and human well-being (van de Water et al. 2022a, and references therein).

Artificial water provisioning may have the largest unintended consequences on elephant demographics (reduced mortality during drought or heatwaves), and the greatest impact on vegetation from higher elephant densities (Smit et al. 2007a). It will become more important to understand this as elephant densities increase in some parts of their range, such as southern Africa, especially with the anticipated large temperature increases caused by global warming (IPCC 2019), and associated effects such as heat stress (Ncongwane et al. 2021). Water provisioning may mitigate the natural mortality that would occur under such conditions, preventing natural population reduction, but may also, potentially, increase the need for other management interventions to deal with the consequence of water provisioning (Chamaille-Jammes et al. 2007a; 2007b; Smit et al., 2007a; 2007b).

Finally, Slotow et al. (2021)'s assessment of the legal context for culling emphasizes the importance of considering elephant welfare and wellbeing in management, as this is both a legal obligation in South Africa (and many other countries), but also linked to the Human Environmental Right in the South African Constitution. The importance of animal welfare is also highlighted in the sentiment analysis conducted by Hammond et al. (2022). Slotow et al. (2021) recommend requiring an ethics review process for all conservation management implementations and interventions involving well-being risk to animals, such as is required for animal research. This is an aspect that has, to date, received scant consideration in elephant management, and should be given more prominence.

A key element missing in decision-making from elephant conservation and management is moderating the use of nature in accordance with widely accepted values, aspirations and rights, and applying the moderating filters of good governance, environmental justice, intergenerational legacy, and human rights (van de Water et al. 2022a). Elephant conservation and management strategies can be contentious, and discussions are often polarized as views and values of stakeholders diverge widely (van de Water et al. 2022a, and references therein). Given the increasing human population, habitat loss, increasing HEC, and shifting local community and global sentiments towards elephant conservation and management, careful consideration needs to be given to the use of direct relative to indirect management interventions. Broader scale planning, including measures to increase the connectivity of fragmented populations, and combined with indirect interventions, may be more environmentally, socially, and economically sustainable than direct interventions. More meaningful and structured engagement by all stakeholders is needed to resolve contentious issues in elephant management (Biggs et al. 2017).

Lastly, there are many beneficial consequences of elephants for humans (van de Water et al. 2022b); and as many of these are poorly documented we suggest this as a focus for future research.

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