Effects of management intervention on elephant behaviour in small, enclosed populations.

by

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DOCTOR OF PHILOSOPHY

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ABSTRACT

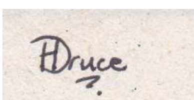
The continual increase in elephant numbers across southern Africa raises concern, though the interventions to manage these populations are more contentious. Within small, enclosed reserves active management is necessary to limit elephant impact. Various management tools exist with which to control fluctuations in elephant population numbers or density and simulate natural large stochastic events to control population growth. During this study, undertaken in the Munyawana Conservancy, KwaZulu-Natal, and Pilanesberg National Park, North West Province, South Africa, several management options were implemented. In order to lower the population numbers, family groups were translocated from the Munyawana Conservancy to other reserves, while to reduce population growth rate an immunocontraception was implemented. Both conservation areas introduced older bulls to normalise the bull population age structure, and expanded the conservation area by inclusion of new land to reduce population density. The influence of these management interventions on the elephant population were measured by their social, behavioural, spatial and movement responses. The older bull introduction was successful as bulls set up exclusive bull areas. There was a quick, subtle affect on the bull groups' size immediately after the older bull introduction, while there was no immediate change within the resident bulls' musth behaviour or duration. During area expansion, elephants appeared to perceive the new unexplored area as a threat although this threat became reduced through time as they became more familiar with it. The spatial scale of response was relatively small, while the temporal scale of response was relatively large. Rotational immunocontraception was shown to be a successful tool to alter herd structure by aging the population and maintaining a low population growth rate. The process of immunocontraception darting had no significant effect on herd associations and movement rates, accordingly the duration of the disruption effects were short lived. During multi-management interventions, no differences were found within the elephant social grouping. Management interventions may pose unforeseen social risks and different populations may respond differently to management induced stress. Therefore, interventions need to be considered for each elephant population which will achieve the conservation area's objectives with the most effective outcome, but with lowest holistic impact.

Keywords: conservation, adaptive management, management interventions, natural process simulation, behavioural risk indicators.

PREFACE

The fieldwork described in this dissertation was carried out in the Phinda Private Game Reserve, which is a part of the Munyawana Conservancy and in Pilanesberg National Park, through the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville, from March 2003 to December 2010. This work was performed under the supervision of Professor Rob Slotow.

This study represents original work by the author and has not otherwise been submitted in any form for any degree of diploma to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.



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DECLARATION 1 - PLAGIARISM

I, Heleen Druce, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

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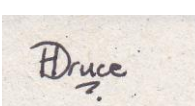

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis:

Publication 1

Druce, H., Pretorius, K., Druce, D. and Slotow, R. (2006a). The effect of mature elephant bull introductions on resident bull's group size and musth periods: Phinda Private Game Reserve, South Africa. *South African Journal of Wildlife Research* 36: 133-137.

Author contributions:

HD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. KP contributed with initial field collection methods. DD contributed to the analyses and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 2

Druce, H., Pretorius, K., Druce, D. and Slotow, R. (2006b). The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. *Koedoe* 49: 77-84.

Author contributions:

HD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. KP contributed with initial field collection methods. DD contributed to the GIS analyses and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 3

Druce, H.C., Pretorius, K. and Slotow, R. (2008). The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation* 141: 3127-3138.

Author contributions:

HCD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. KP contributed with initial field collection methods. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 4

Druce, H.C., Mackey, R.L. and Slotow, R. (2011). How immunocontraception can contribute to elephant management in small, enclosed reserves: Munyawana population as a case study. *PLoS ONE* 6(12): e27952. doi.10:1371/journal.pone.0027952.

Author contributions:

HCD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. RLM contributed to the statistical analyses, modelling and provided valuable comments on the manuscript. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 5

Druce, H.C., Mackey, R.L., Pretorius, K. and Slotow, R. (*in press)*. The intermediate-term effects of PZP immunocontraception: Behavioural monitoring of the treated elephant females and associated family groups. *Animal Conservation.*

Author contributions:

HCD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. RLM contributed to the statistical analyses and provided valuable comments on the manuscript. KP contributed with initial field collection methods and initiated the immunocontraception methods. RS contributed to the design of the paper and provided valuable comments on the manuscript.

Publication 6

Druce, H.C., Shannon, G., Mackey, R.L., and Slotow, R *Unpublished*. The effect of management interventions on elephant assayed at the population and breeding group levels.

<u>*Author contributions*</u>*:*

HCD conducted all fieldwork, processed and analysed the data, and designed and wrote the paper. GS contributed to the design of the paper. RLM contributed to the statistical analyses. RS contributed to the design of the paper and provided valuable comments on the manuscript.

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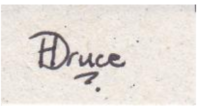

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A time with elephants; the day Dumbe was born.

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CHAPTER 1
GENERAL INTRODUCTION

Greater species diversity and a high genetic diversity within species ensure natural sustainability for all life forms (IUCN 2012). The common threats to biodiversity are human population explosion and over exploitation of natural resources, human development, climate change and global warming. Using resources faster than they can regenerate and creating waste such as CO_2 faster than it can be absorbed, causes an ecological overshoot, where after it adds to the pressure of climate change and global warming (WWF 2012). Maintaining healthy biodiversity can play a significant role in climate change mitigation and therefore the world's protected areas are essential in safeguarding this role (IUCN 2012).

Africa is the world's second largest continent with enormous landmass filled with great biodiversity, abundant variety of landscapes, a wide range of habitats and a high diversity of flora, micro-, macro- and megafauna (Joyce 1999). The biodiversity value that Africa adds on a global scale is crucial and therefore the preservation, protection and conservation of natural diversity is vitally important.

Historically, wildlife used to roam freely throughout Africa, with natural occurrences of fluctuations within species population numbers, due to droughts, poaching, hunting, predation and the natural migration of animals between open conservation areas, which kept animal numbers low enough not to cause irreversible damage to the environment (Ottichilo 1986, 1987, Whitehouse and Schoeman 2003, Wittemyer et al. 2005). Wildlife management and protection of wildlife were historically either non-existent or based on a hands-off approach (Bothma 2002). Uncontrolled, excessive and illegal hunting and poaching reduced some species to the brink of extinction. During later years, the wildlife management approach shifted to active manipulation and many of these nearly extinct species' survival was ensured by confinement within small, enclosed protected conservation areas. However, confinement of animals within small, enclosed conservation areas requires that they be actively managed (Burke 2005) as these populations are prevented from natural immigration or emigration (Novellie et al. 1991). Traditionally managers of enclosed conservation areas have provided artificial water points (Brits et al. 2002) and undertaken controlled burning programs (Brockett et al. 2001) in order to stimulate new plant growth. Consequently, resources within these enclosed areas were hardly ever limiting factors. Such resource provisioning in conjunction with limited natural enemies and diseases may result in steadily increasing animal populations. However, a high density of animals can cause a negative effect or impact on the environment, with the result that active management is required in order to conserve biodiversity as a whole, rather than individual species. Currently, the focus of wildlife management is on an adaptive management approach, which ensures continual assessment of management outcomes, while allowing learning and adapting strategies to achieve optimal outcomes, for example the Kruger National Park and surrounding private game reserves (Grant et al. 2011).

Selective and active management interventions can be used effectively within fenced, small, enclosed conservation areas to simulate natural processes such as predation or episodic catastrophic events (e.g. drought), which naturally regulate population densities. Within natural, open conservation systems, predation and large stochastic events such as drought, fire keep populations at a sustainable level by eliminating the old, weak and young (Owen-Smith et al. 2005, Foley et al. 2008, Woolley et al. 2008a, Woolley et al. 2008b). However, within modern conservation areas, especially small, enclosed reserves, natural stochastic events are altered by human management interference (Woolley et al. 2008a), with more intervention required for smaller reserves (Kettels and Slotow 2009). In order to simulate natural processes within these conservation areas through the use of management interventions, immunocontraception can be used to regulate calf recruitment, for example, and selective hunting or culling can be used to eradicate old or sick individuals from the population.

Adaptive management should simulate natural processes to achieve management objectives without a negative effect on the system (Walker 1998). However, because active management requires managers to imitate the processes of nature (Caughley 1976), it can often have unforeseen consequences for example the killing of white rhino, *Ceratotherium simum*, by elephant (Slotow et al. 2000). This is of special concern for species with complex social systems, for example baboons, *Papio hamadryas* (Krebs and Behlert 2006, Rijksen 1981), lion-tailed macaques, *Macaca silenus* (Singh and Kaumanns 2005) and elephants (Slotow et al. 2000, Whitehouse and Kerley 2002). Thus, for adaptive management to be effective and non-detrimental, a sound understanding of the natural processes is required.

Socially-complex, gregarious, long-lived species are sensitive to disruption of their social dynamics and often shown a response to external stresses (Lussue 2007, Parson et al. 2009), therefore they can be a challenge to conserve and manage. Several studies on socially-complex species such as humpback whales (*Megaptera novaeangliae*: Weinrich and Corbelli 2009), bottlenose dolphins (*Tursiops truncates*: Williams et al. 2002; Lusseau 2004, Hawkins and Gartside 2009), mountain gorilla (*Gorilla gorilla*: Robbins et al. 2009) and grey wolves (*Canis* *lupus*: Blanco and Cortes 2007, Lovari et al. 2007, Weiss et al. 2007) suggest changes in their feeding, breeding behaviour and spatial movement due to human disruption and pressure. African elephant's (*Loxodonta africana*) social grouping may change when elephant are under management intervention pressure (e.g. hunting (Burke et al. 2008); female immobilisation (Burke 2005), poaching (Andersen and Eltringham 1997, Owens and Owens 2009), or from catastrophic fire (Woolley et al. 2008b)). Sustained pressure, for example, in response to poaching, may result in disruptions to population's demographics, social structure and mating success in the long term (Bradshaw et al. 2005, Gobush et al. 2008, Ishengoma et al. 2008). Certain scientific studies have shown that poaching activities influence elephant home ranges extensively (Aleper and Moe 2006), while hunting activities cause a movement avoidance effect (Burke 2005). African elephants have also been found to increase their group sizes (Eltringham 1977) and move into protected areas (Western 1989) in response to intense poaching activities. It has also been documented by Douglas-Hamilton et al. (2005) that the elephant population in all Kenya corridor reserves 'streak' through corridors mostly at night time due to human settlements along the corridor areas and in order to avoid human interference. Therefore, management interventions may pose a risk to the species' from an ecological, social and welfare perspective.

Wildlife management and decision-making needs to take into account the ecological processes of ecosystems and their biodiversity, as well as their socio-political and economical values (Biggs et al. 2008), especially with a socially-complex, gregarious, long-lived species such as elephants (Douglas-Hamilton and Douglas-Hamilton 1975, Moss and Poole 1983, Slotow et al. 2005). Conservation management should therefore consider management interventions for the intended scenario with the most effective predicted outcome, but with the least holistic impact (Sukumar 2003). However, any management strategy or intervention might have a potential uncertain, unforeseen risk component (Slotow et al. 2008). It is important to incorporate social structure and behaviour into risk assessment of interventions and management decision-making, to accurately evaluate the persistence of social species and the influence of human interventions (Parson et al. 2009). This understanding and knowledge of behaviour is then essential for developing tools that are required for the most effective management of the species with the least negative impact (Singh and Kaumanns 2005).

Historically, the African elephant (*Loxodonta africana*) was a species in decline and almost on the brink of extinction due to poaching and over-exportation of ivory for the ivory trade. This resulted in the Convention on International Trade in Endangered Species of Wild Fauna and

Flora (CITES) placing elephants on Appendix II in 1977, which later shifted to Appendix I in 1990, enforcing an international ban on all cross-border trade of ivory and other elephant products (IUCN 2006).

Today, the once wide distribution of the African elephant throughout South Africa is limited to fenced conservation areas, reserves and zoos. Competition and conflict between man and elephant for space has lead to the decline of elephant numbers outside conservation areas. In 1998, an estimated 11 905 elephants were left in confined and fenced areas in South Africa (Barnes et al. 1999). During the past decade, there has been a rapid increase in the number of small reserves (<1000 km^2) in South Africa (Druce et al. 2004, Slotow et al. 2005). This in conjunction with a moratorium on culling in South Africa has resulted in the elephant population in South Africa growing to an estimated 17 847 by 2007 (CITES 2008). Although some of these reserves have been developed to enhance biodiversity conservation, many of them exist for the eco-tourism industry and to benefit from the large mammals within their boundaries (van de Merwe and Saayman 2003, Grant et al. 2011). Tourism entails the reintroduction of valuable viewing species into these reserves sometimes regardless of the ecology and sustainability of these and other species (Blignaut et al. 2008). The elephant is one of the key species in the ecotourism industry, possibly because of their sheer size, charisma, intelligence, social complexity or just the potential danger associated with them. Because elephant reintroductions have occurred into small, enclosed reserves, they need to be actively managed (Slotow and van Dyk 2004) to prevent overpopulation and so that their perceived negative impact on the vegetation can be minimized (Anderson and Walker 1974, Herremans 1995). There is also a need to ensure that genes can be exchanged between enclosed areas, while most importantly, elephants also need to meet all their social and behavioural needs within these areas.

Management interventions

Over the last 20 years, translocation of elephants to small, enclosed reserves has been a welcome option for removing surplus elephants from reserves, mainly Kruger National Park, in South Africa (Garai et al. 2004). Between 1979 and 2001, over 800 African elephants were translocated to over 58 reserves in South Africa (Garai et al. 2004). This has resulted in 'the elephant problem' being created in these reserves as the elephants are now trapped in small conservation areas with limited natural population fluctuations or migrations.

Traditionally elephant populations were controlled by culling in Kruger National Park, South Africa, as in some other southern African countries (Child 2004, Pienaar 1969, Poole 1993, van Aarde et al. 1999). Culling is a planned reduction of the population by the eradication of a large number of elephants to achieve some predetermined population level (Owen-Smith 1988). Culling was carried out between 1967 and 1990 in the Kruger National Park, South Africa, through a remote intra-muscular injection of the compound Scoline (succinylcholine chloride) from a helicopter (Whyte et al. 1999). However, due to the physiological processes involved, this method was deemed an inhumane way of killing elephants, as the animal in effect suffocates to death whilst being fully aware of it. This method was then improved by initially darting elephants with Scoline, and then brain shooting the animal as soon as people could get to the animal and before suffocation would be experienced. However, the elephants were not always found in time before the suffocation process commenced. This method was then refined further and evolved into a single brain shot from a helicopter per target individual. Culling operations disrupted population dynamics, movement patterns and intensified the local impact of elephants (van Aarde et al. 1999). Another concern associated with previous culling operations were that only the adult elephants were killed, while the youngsters were used to supply the demand of new, smaller reserves with elephants. At the time of these introductions, technology permitted only elephants of a maximum shoulder height of 2 m (i.e. 8-10 years old) to be translocated. With these orphan introductions, the youngsters later displayed behavioural abnormalities (Slotow et al. 2000). Culling in the Kruger National Park was discontinued during 1995 (van Aarde et al. 1999) due to increasing public pressure and a lack of proof of the detrimental destructive effect of elephants (Carruthers et al. 2008). While culling remains a controversial subject, management authorities such as South African National Parks may consider and undertake culling again as a future management tool. Future culling operations will be done more efficiently with a single brain shot per individual from a helicopter and with as little as possible impact or influence on the remaining population (i.e. culling of a complete family unit at once). According to the National Norms and Standards for the management of elephants in South Africa, culling should be used as the last resort management action, once all other actions have been considered and rejected (DEAT 2008).

Translocation is seen as a more humane method of controlling elephant population numbers and lowering elephant densities. Individual elephants are translocated from an area with a high elephant density to an area with low elephant density (Garai et al. 2004). While ethically appealing, translocation is not a practical solution for reducing numbers in large over-populated areas. Transporting entire elephant family groups is both expensive and cumbersome, but more importantly, there are few existing conservation areas that can still accommodate extra elephants in southern Africa (Whyte 2004). On several reserves, reintroduced elephants have exhibited aggressive and social behavioural abnormalities, due to a disruptive social system during introduction (Slotow et al. 2000, Bradshaw et al. 2005). Prior to 1994, translocation focused on moving surplus, orphaned juvenile elephants, from culling operations (Garai et al. 2004). As the importance of the elephant social system became better understood, and simultaneously technology, equipment and expertise improved, translocations shifted to only adult bulls and entire family groups. To attempt to resolve the social and behavioural abnormalities within previously introduced 'culled orphan' populations, older mature individuals have been successfully introduced into the resident young population (Slotow et al. 2000). The introduction of older mature adults is a method by which to normalize skewed age structure and stabilize the socially disruptive behavior of the younger individuals. To ensure effectiveness after translocation, the new resident population must be monitored and managed to prevent overpopulation within the new area, especially because most translocations are from larger to smaller reserves.

As enclosed elephant populations cannot disperse and migrate as a result of fences, increasing the size of conservation areas is a popular option to deal with increasing elephant densities. The option of buying more land neighboring already existing reserves and dropping fences between properties to create bigger conservation areas appears to be the most ethical, practical and hands-off management strategy. Expansion with undeveloped natural land is the best option, however this management option of enlarging conservation areas might not always be feasible, because undeveloped land is limited and could be expensive to acquire. Furthermore the developed land that surround conservation areas are normally refer to as communal tribal lands, which consist of a mosaic of homesteads and grazing lands. The possibility exist for communal land adjacent to protected areas to serve as 'sink' areas for elephants to disperse from high density areas, within a metapopulation management approach (Van Aarde and Jackson, 2007). This may assist with socio-economic growth, as conservation and tourism create a secondary economical benefit from elephants for local rural communities, such as employment and training. However since parks employ a relatively small proportion of the neighboring population, communities have expectations of greater access to other economic benefits from parks, such as direct economical benefits from elephant culls or hunts (Twine and Magome, 2008). Where conservation areas can be increased in size, elephants can disperse and reduce the degradation of vegetation in localized areas. However, historical records show that elephants remain within their known home ranges and that the colonization of vacant, new areas may only occur at an average of 7-10 kilometers a year (Whyte 2001). Consequently, any migration that may occur will happen very slowly. However, many studies have also shown that animals adapt their ranging and forging behaviour to avoid unexplored, unknown areas and human-induced disturbance (Burke 2005, Douglas-Hamilton et al. 2005, Maude 2005, Aleper and Moe 2006). Once a conservation area is expanded, it appears to be perceived by resident animals as a threat and they act cautiously in exploring the new area. The cautious behaviour has been validated by numerous studies (Boone and Hobbs 2004), including by African elephants (Douglas-Hamilton et al. 2005) that have shown that animals adapt their ranging and foraging behaviour to avoid unexplored areas and human-induced disturbance. Further studies have shown that fences cause change in habitat selection and intensify the pressure on the resources by elephants (Loarie et al. 2009, Vanak et al. 2010). Therefore, although the enlargement of conservation areas may be a popular management option at present, effects for increasing elephant populations may only be seen in the long-term.

Other population control methods, which have been developed over the last few years, include sterilization and contraception. Sterilization of elephant bulls involves a surgical laparoscopic operation during which a section of the vas deferens is removed. The laparoscopic surgical operation of elephant cows involves permanently restricting the blood supply to the ovaries. Sterilization as a management method is extremely expensive, the operation is time consuming, irreversible and needs sophisticated expertise (M. Stetter, Disney Animal Kingdom, personal communication). Sterilization can only ever be a population control for small, enclosed reserves, due to the scope of the logistics of this intervention.

Contraception can control birth rates and thereby reduce the population growth rate, by lengthening inter-calving intervals or by increasing the age that females produce their first calves. Contraception does not reduce the existing elephant population, therefore it would not be effective to use for immediate effects within on an already overpopulated conservation area. However, by using contraception in the long-term to prevent or slow population growth, it results in an aging affect on the population and therefore over time will result in a reduction of the population size as older animals die at a faster rate than births into the population. The efforts needed to stabilize elephant numbers in entire large populations through birth control are not realistic, because at the population level, birth control is constrained by the large number of females needing treatment, the frequency per individual to ensure the effectiveness, financial and logistical constrains. As Bertschinger et al. (2005) state, immunocontraception is only suitable, effective and manageable for small to medium sized, confined populations. However a proportion of females within a large population can be treated which will still result in a reduction of the overall population growth rate.

Two methods of contraception on females have been researched during the past few years. The one method is hormonal contraception, which is a slow release oestradiol implant under the skin (Whyte and Grobler 1998). Monitoring of the treated individuals has shown that the hormonal disturbance arising from the high level of circulating oestrogen makes the method ethically unacceptable in its present form. Treated cows are induced into a state of false oestrus and are therefore attractive to bulls. The constant attraction of bulls drives the cows away from their still dependant calf and family groups. Monitoring of these animals has suggested that this results in increased mortality of the calves (Butler 1998). Because of these side effects and the hormonal imbalance, hormonal contraception for elephants was found to be unacceptable and inhumane to use, and was therefore discontinued.

The second method is immunocontraception, which was first developed in the mid-1980's by Dr. Irwin Liu of the University of California. The immunocontraceptive is Porcine Zona Pellucida (PZP), which is the porcine (domestic pig) version of a protein (ZP, or Zona Pellucida) that surrounds the eggs of all mammals and is extracted from pig ovaries (Rutberg 1998). Rutberg (1998) explains that the sperm must lock onto the ZP protein before they can penetrate the egg. The immune system of animals (apart from pigs) injected with PZP respond by producing antibodies to attack this foreign protein. In females, these antibodies latch onto their own ZP proteins, thereby preventing the sperm from attaching and subsequently prevent fertilization (Rutberg 1998). PZP has been developed, applied and proven to be effective in controlling reproduction in a variety of captive zoo species (Kirkpatrick et al. 1995) and wild animals, including white tailed deer (Mcshea et al. 1997), feral horses (Kirkpatrick et al. 1990), and more recently, the African elephant (Fayrer-Hosken et al. 1997, Fayrer-Hosken et al. 2001, Delsink et al. 2002). Elephant immunocontraception field trials have successfully been completed with no elephants becoming pregnant (Delsink et al. 2005). As immunocontraception is a non-hormonal contraceptive, elephant females display normal oestrous cycles (Delsink et al. 2002). The PZP vaccine only causes an immune response and therefore works effectively on pregnant females, with no effect or harm to the unborn (Kirkpatrick et al. 1990, Fayrer-Hosken et al. 2001). Consequently, it has been suggested that immunocontraception can be used to stop elephants from breeding, or to prolong the calving intervals of each individual female and therefore slow down population growth. Immunocontraception is safe and reversible and can be used as a practical management tool for controlling elephant populations (Fayrer-Hosken et al.

2001) in small, enclosed conservation areas. However, limited behavioural studies have been undertaken to determine if there is any change in the behaviour of contracepted cows or the effects on the population of limited or no births over a long time period.

Concerns have been expressed regarding the ethics involved in animal management strategies (Lecocq 1997, Moberg and Mench 2000). Little is known about the influence and effect that various management decisions and actions have on wildlife, especially elephant populations' demographics, social and behavioural activities and movement rates. The effect of direct human intervention on populations should be established and limited to the management strategies with limiting induced behavioural altering influences and the least physiological stress.

This study aims to determine the influence and effects of various management interventions on the elephant population's demographics, social behaviour, spatial and displacement responses within an enclosed reserve and to answer wildlife managers' concerns by determining the duration of the effect of disruptions on the elephant population after management activities. There are limited comparative studies that have investigated the effect of human disturbance on the African elephant. Therefore, the objectives of this study are to quantify the direct effect of the introduction of mature bulls (i) on the resident bulls group size and musth periods, (ii) on the resident bulls ranging patterns, (iii) to determine the response of the existing population to conservation area expansion, (iv) to test the effectiveness of immunocontraception as a management tool and (v) to determine the elephant population's behavioral response to the immunocontraception application. Finally the study aimed (vi) to determine the social behavioral response of elephants to various management interventions.

African elephants' social organization

The basic unit of African elephants' social organization is the family unit, which is made up of mature females and their calves (Laws and Parker 1968, Douglas-Hamilton 1973). Female elephant society consists of complex multi-tiered relationships extending from mother-offspring to family units, bond groups and clans (Poole 1996). Family units of elephant can form aggregations for an indefinite period of time, which number in the thousands. The female elephant society is fundamentally matrilineal, as the oldest female has the status of the matriarch. The role of a matriarch is a leadership role and influences every aspect of the family's daily routine, including movement and seasonal dispersal. As the matriarch is the oldest in the family group, she has the greatest amount of social and historical knowledge (Archie et al. 2006).

Females born into the family unit remain in their natal herd their entire lives, whereas males leave or are forcibly ejected from their natal family group shortly after reaching puberty, which is usually between the age of 14 and 17 years (Poole et al. 1984, Poole 1989). These bulls will then join older bulls, form bull groups and establish bull areas away from breeding herds. Within these bull groups, male association is random, with bulls not forming any long-term bonds with other individuals (Laws and Parker 1968, Moss and Poole 1983). Males in musth leave these bull groups in search of females in oestrus to mate with and only return to the bull areas after their musth periods. Musth is a state of heightened sexual and aggressive activity in male elephants (Poole 1987), is associated with high levels of testosterone secretion (Poole et al. 1984) and is characterized by a distinct posture, swollen and secreting temporal glands, urine dribbling and increased sexual and aggressive behaviour (Poole 1987, Slotow et al. 2000). Interaction intensity differs between bulls depending on their sexual state, with interactions between sexually active males tending to be more aggressive (Poole1989). Males gradually enter musth as they become older and more experienced or more dominant (Poole 1989, Slotow et al. 2000). In natural populations, musth first occurs between 25 and 30 years of age and its duration increases with age (Poole 1987, Slotow et al. 2000). In young bulls it can last a few days, while in 40 year old bulls, musth can last up to four months. Young bulls in a natural population lose the physical signs of musth shortly after an aggressive interaction with a higher-ranking musth male (Poole 1987, Slotow et al. 2000). As a result, larger males may delay the onset of musth in young males (Poole 1987, Slotow et al. 2000).

Females on the other hand reach sexual maturity as early as 8-12 years and will typically produce their first calf 22 months later (Sikes 1971, Owen-Smith 1988, Poole 1994, Mackey et al. 2006). The only time that female elephants will mate is during their oestrus periods. Studies in Amboseli, Tanzania have shown that females come into oestrus and conceive approximately 3.5 years after the birth of their previous calf (Moss 1983). Female elephants experience very short oestrous cycles of two to eight days (Moss 1983), but on average females come into oestrus for four days (Moss 1988). According to Moss (2000), an individual elephant cow might produce a calf every four years from the time she is 13 years until she is in her fifties (females reach menopause at approximately 50 years of age (Owen-Smith 1988, Moss 2001)), so she may give birth to as many as 12 calves in her lifetime. Many studies have shown that the inter-calving interval of cows is between four to five years (Moss 1988, Owen-Smith 1988, Moss 2000), however recent studies in enclosed populations in South Africa have calculated calving intervals at between three and four years (Mackey et al. 2006). At every birth within the family group there is great excitement and support from the related females as a result of the very strong social bonds within the elephant family groups.

Although the behaviour and social organization of the African elephant has been studied thoroughly for many years, little is known about the effects of human disturbance and management activities on enclosed populations.

Study Area

This study was conducted within the Munyawana Conservancy (MC) which is located in KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E). Initially Phinda Private Game Reserve (Phinda) was established in 1991, and encompassed an area of approximately 150 km^2. During August 2004, the boundary fences between Phinda and two neighbouring reserves, Zuka and Mziki Pumalanga were removed, forming the Munyawana Conservancy, with an area of 185 km^2. During May 2006 the boundary fences were removed between Munyawana Conservancy and the neighbouring reserve Sutton, increasing the area of the Conservancy to 207 km^2.

The vegetation types within the Munyawana Conservancy, according to Mucina and Rutherford (2006) are Sand Forest, Southern Lebombo Bushveld, Zululand Lowveld, Western Maputaland Clay Bushveld, Makatini Clay Thicket, Maputaland Coastal Belt and Subtropical Salt Pans. One perennial river, the Mzinene River, flows from West to East through the southern section of the conservancy and dams are extensively distributed throughout the properties. During the rainy season, surface water is extensive, and while some of the dams retain water all year round, other dams are supplied with borehole water during the dry periods. The Munyawana Conservancy has a summer rainfall regime and temperatures range from an average minimum of 10 °C in winter to an average maximum of 35 °C in summer.

Prior to the proclamation of Phinda as a game reserve, the land was carefully managed and restored from former livestock farming and pineapple farms back to a semi-natural state. Thereafter, hundreds of large mammals including elephant, lion (*Panthera leo*), cheetah (*Acinonyx jubatus*) and white rhino (*Ceratotherium simium*) were reintroduced into the reserve from 1991. During the end of 2004, black rhino (*Diceros bicornis*) were also introduced into the reserve as a part of the WWF's Black Rhino Range Expansion Project. The main revenue for the reserve comes from eco-tourism. The company managing Phinda, &Beyond, uses their conservation initiative to support, educate, involve and develop the local communities in the areas surrounding the reserve.

Secondly, Pilanesberg National Park (PNP) is located in North West Province, South Africa (25°8' - 25°22' S and 26°57' - 27°13' E). The reserve was established in 1979, with an area of approximately 500 km^2 and later increased to 570 km^2 by the end of 2008. The park is circular in shape, is located in the crater of an extinct volcano, and as such has hilly savanna relief (Burke 2005). The park falls within the transition zone that lies between the Kalahari Thornveld in the west and the Bushveld in the east. The habitat type is classified as sourveld, dominated by Acacia and broad-leaf bushveld growing on rocky mountains and hills. The habitat ranges from closed thickets to open grasslands (Acocks 1988). The park consists of one major river system running through the centre, various ephemeral tributaries, one large central dam and pumped water points which are distributed throughout the reserve. The annual rainfall is 630 mm with a range of 480 mm to 1000 mm, which falls mainly in the summer months. Temperatures range from an annual mean minimum of 5 °C to an annual mean maximum of 31 °C.

Prior to its proclamation as a reserve, the Pilanesberg Complex was depleted of game populations and degraded as a result of commercial farming practices. During 1979, over 6000 head of game were re-introduced (Boonzaaier and Collinson 2000). Since the reclamation and development of the reserve, it has become fully stocked with the ‘big five’ and other rare and endangered species like the African wild dog (*Lycaon pictus*), brown hyaena (*Hyaena brunnea*) and sable antelope (*Hippotragus niger*). There are wilderness areas situated within the park with minimal tracks and inaccessible areas. The tourist area of the park comprises approximately 50% of the park, with self-drive tourist and concessionaires that offer guided game drives, walks and balloon flights (Burke 2005).

Study populations: dynamics and history

The core of the Phinda elephant population was introduced as orphans from culling operations (approximately 10 years of age at introduction) in Kruger National Park between 1992 and 1994. During 1994 a further four adult elephants (approximately 20-25 years of age at introduction) were introduced from Gonarezhou National Park, Zimbabwe. In June/July 2003 a total of 37 elephants in four different family groups were translocated from Phinda to other reserves in South Africa. Three older bulls from Sabi-Sands in Limpopo Province were introduced into Phinda during 2003. The first two bulls (aged 29 and aged 36) were introduced into an electrified holding boma in Phinda on 12 July 2003 and released into the reserve on 14 July 2003. A third bull (aged 41) was introduced into the boma on 1 August 2003 and released into the reserve on 8 August 2003. Prior to the bull introduction in 2003, there were a total of 16 resident bulls that were independent of the family groups, one of which was 36 years old and 15 younger bulls ranging in age from 15 to 26 years old. In July 2006 the total Phinda elephant population was 88 individuals, consisting of the 19 independent adult bulls (including the three older introduced Sabi-Sands bulls) and five family groups. For the purpose of this study, an 'independent family group' is defined as a stable group of adult females and their offspring consistently led by a matriarch (Lee 1987). Zuka also contained a small group of 4 young elephants (two bulls and two cows <7 years old at introduction in 1996), but at the end of 2005 a single bull from the Zuka population was found dead on the Zuka property, the cause of death was unknown. The farm Sutton contributed a single, small family group consisting of seven individuals (introduced in 2001) to the Munyawana Conservancy, which resulted in a total population of 98 elephants at July 2006.

The elephant monitoring in Phinda was initiated as a result of growing concern over the high density of elephants within the reserve and the possible negative impact on the rare Sand Forest vegetation. Monitoring began on the Phinda elephant population in March 2003 with no monitoring on the populations within the other reserves until their inclusion into the conservancy. Since then monitoring has been ongoing on the entire Munyawana Conservancy elephant population. The initial monitoring focused on identifying the whole elephant population and determining their population dynamics. All adult female and male elephants in Phinda population were identified through unique characteristics and identification templates were drawn for each individual. The cow-calf relationships and family group structures within the Phinda population were determined. This population dynamics information was necessary and valuable for monitoring the effects of the range of elephant population management decisions that were undertaken during this study. Although studies are ongoing on the Munyawana elephant population, only data from March 2003 to July 2006 were used for this study. Furthermore, only the elephants that were originally introduced into Phinda were used in all analyses, with the elephants from the other reserves which were included in the Munyawana Conservancy only being included in the analysis of the immunocontraception plan.

The first elephants were introduction into Pilanesberg National Park in 1979, when 8 elephants were translocated from Addo Elephant National Park. However, 7 of the introduced elephants died and only one survived. A total of 76 orphan elephants were introduced from Kruger National Park between 1981 and 1993 (orphaned from ex-culling operations). Another two elephants were introduced from Namibia in 1982 (juvenile male and juvenile female). During the same year, two tame circus-trained 19-year old elephants were introduced from USA and assumed the role of matriarchs in the Pilanesberg herds. The Pilanesberg orphan population formed two breeding herds lead by the two older tame females. In 1997, other older females started to break away to form smaller family groups. During 1992 two more young males were introduced from Mabula and were subsequently removed in 1993. Six older males (26-36 years of ages) were introduced from Kruger National Park during 1998. During 1979–1998, 94 elephants were introduced (excluding the two Mabula males).

Primarily, studies of Pilanesberg elephants focused on bulls, as a major concern was that bulls were causing both black and white rhinoceros mortalities with the park (Slotow and van Dyk 2001). Individual adult bulls were identified and assigned an identification template. Management culled fourteen of the males that were culprits of rhino killings and a further 15 elephants died between 1979 and 2001 of other causes (Slotow and van Dyk 2001). The six older bulls were introduced from Kruger to normalise the population age structure among the bulls. This successfully suppressed the resident bulls' unwanted behaviours (Slotow et al. 2000). The ranging patterns of these were analysed (Slotow and van Dyk 2004). From 2000, the elephant monitoring programme began to focus on the breeding herds and the entire population demographics (Burke 2005). By September 2005, the PNP population totalled 165 individually identified elephants, of which 37 were independent adult bulls and 128 were part of 18 relatively stable matriarchal family groups (Woolley et al. 2008b).

CHAPTER 2
THE EFFECT OF MATURE ELEPHANT BULL INTRODUCTIONS ON RESIDENT BULL'S GROUP SIZE AND MUSTH PERIODS: PHINDA PRIVATE GAME RESERVE, SOUTH AFRICA.

Abstract

African elephant have been reintroduced into small, enclosed reserves in South Africa, many populations being established with orphans <10 years old. This has resulted in abnormal behaviour in some elephant populations, which was corrected in Pilanesberg National Park by introducing older bulls and culling certain problem elephants. In July 2003, three older bulls (29 to 41 years old) were introduced into Phinda Private Game Reserve, KwaZulu-Natal, South Africa in order to normalise the bull age structure and in an attempt to reduce the abnormally long musth period of one particular resident bull. These introduced bulls were monitored intensively after release, as was the resident bull population, both before and after introduction of the older bulls. The introduced bulls all came into musth within eleven months post release. The older bulls do not appear to have had any influence on the musth periods of the oldest resident bull (36 years old at introduction). Detailed behavioural studies of the effects of management actions on elephant populations, within small, enclosed reserves provide information and resources for future management decisions. This study demonstrates that old bulls can be successfully introduced to very small areas, with no detectable medium-term (1 year) effect on the behaviour of a relatively dense population of resident elephants.

Keywords: *Loxodonta africana*, adaptive management, musth duration, social behaviour

Introduction

The African elephant (*Loxodonta africana*) is one of the most charismatic species in the ecotourism industry in southern Africa (Slotow and van Dyk 2004) and as a result, many state and private game reserves have reintroduced elephants, many of which were orphaned elephants originating from culling operations in Kruger National Park (Garaï et al. 2004). However, these reserves are small (<1000 km^2) and surrounded by electric fences, essentially acting as an enclosed system, preventing the immigration and emigration of large mammals. As a result, elephant populations within these enclosed reserves need to be actively managed (Slotow and van Dyk 2004) to ensure that reserves do not become overpopulated, that genes can be exchanged, that elephants can meet all of their social, behavioural and other needs (Garaï et al. 2004), and so that the perceived negative impact on the vegetation by elephant (Anderson and Walker 1974, Herremans 1995) can be minimised.

The basic unit of African elephant social organization is the family unit. Females born into the family unit remain there upon reaching sexual maturity, while males leave or are forcibly ejected from family groups shortly after reaching puberty, usually between the age of 14 and 17 years (Poole et al. 1984, Poole 1989). These bulls will then join older bulls, form bull groups and establish bull areas away from breeding herds. Males in musth leave these bull groups in search of females and return after their musth period.

Musth is a state of heightened sexual and aggressive activity in male elephants (Poole 1987). The musth period is associated with high levels of testosterone secretion (Poole et al. 1984) and is characterized by a distinct posture, swollen and secreting temporal glands, urine dribbling and increased sexual and aggressive behaviour (Poole 1987, Slotow et al. 2000). Interaction intensity differs between bulls depending on their sexual state, with interactions between sexually active males tending to be more aggressive (Poole 1989). Males gradually enter musth as they become older and more experienced (Poole 1989, Slotow et al. 2000). In natural populations, musth first occurs between 25 and 30 years of age and its duration increases with age (Poole 1987, Slotow et al. 2000). In young bulls it can last a few days, while in 40 year old bulls, musth can last up to four months. Young bulls in a natural population lose the physical signs of musth shortly after an aggressive interaction with a higher-ranking musth male (Poole 1987, Slotow et al. 2000). As a result, larger males may delay the onset of musth in young males (Poole 1987, Slotow et al. 2000).

Pilanesberg National Park experienced great problems during the 1990s when young elephant bulls in musth killed rhinoceros and behaved aggressively towards tourists (Slotow and van Dyk 2001). It was suggested that this problem was due to most of the elephants initially introduced into the system being orphans from culling operations in Kruger National Park. As a result, the young bulls had not grown up in an elephant population with a natural structure or with older bulls that would suppress their onset of musth (Slotow et al. 2000). Pilanesberg management introduced six older bulls, which suppressed the young bulls' musth behaviour and culled problem animals (Slotow et al. 2000). The killing of rhinoceros ended and the elephant problem was solved (Slotow and van Dyk 2001). The results of that study indicated that other reserves with young elephant populations might be able to solve or prevent similar behaviour of their young bulls by introducing older bulls (Slotow et al. 2000) without the need to cull.

Materials and methods

This study was undertaken in Phinda Private Game Reserve, KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E) between March 2003 and December 2004. Phinda was established in 1991, with an area of approximately 150 km^2. The core of Phinda's elephant population was introduced from Kruger National Park as orphans from culling operations between 1992 and 1994. All the individuals were young and within the same age class (approximately 10 years old or younger at introduction). During 1994 four adult elephants, two bulls and two cows (approximately 20-25 years of age) were introduced from Gonarezhou National Park, Zimbabwe. Three older bulls from Sabi-Sand in Limpopo Province, South Africa were introduced into Phinda during 2003. The first two bulls (PH32 - aged 29 and PH33 - aged 36) were introduced into an electrified holding boma in Phinda on 12 July 2003 and released into the reserve on 14 July 2003. A third bull (PH31 - aged 41) was introduced into the boma on 1 August 2003 and released into the reserve on 8 August 2003. In July 2004, the Phinda elephant population consisted of 78 individuals, of which were 19 adult bulls.

Prior to the bull introductions in 2003, Phinda had one bull 36 years old (PH1) and 15 young bulls ranging in age from 15 and 26 years that were independent of the breeding herds. This age structure was unnatural because of the large proportion of young males of approximately the same age. A natural population structure should have individuals spread through the different age groups. Because the oldest resident bull was approximately ten years older than most of the rest of the Phinda bulls, he dominated the other bulls, remaining in musth for long, continuous periods with abnormal displays of aggressive musth behaviour towards other bulls and humans. This was possibly due to no competition or conflict with same age or older bulls. As a result, it was decided to introduce three older bulls in 2003 to create a more natural age structure within the male population, by filling the age gap of bulls older than 25 years. It was hoped this would also suppress the abnormally long musth periods and aggressive behaviour of PH1.

An aim of this study was to determine the effect of the introduction of three older elephant bulls on a young resident bull population, by comparing group sizes and musth periods for selected bulls before, during and after introduction of new bulls to Phinda Private Game Reserve. A further aim was to determine how the three new bulls settled into the reserve by comparing their musth periods and group sizes with those of the resident bulls.

The Phinda elephant population was monitored daily and at each sighting all elephants were identified using master identification templates. At every sighting general location data, the name of adult individuals present and behaviour codes were recorded. If a bull was in musth, separate behaviour and condition data were recorded for the individual. Most observations were made from a vehicle on the existing road network. With the extensive road network on the reserve, observations were regarded as being sufficient, with a total of 347 sightings for five resident bulls for the duration of this study period. However, two of the introduced bulls were fitted with GPS collars, which downloaded GPS positions at set time intervals and transmitted the GPS points to a ground station using GSM cell-phones. These collars were set to download location points every two hours, which were then stored on a master computer. With only two bulls being collared, and located at will, some individual bulls may not have been seen for extended periods. The maximum period that an individual bull was not located was 29 days, but on average, the period between consecutive sightings for an uncollared bull was 3.9 days.

Results and discussion

Group size

Analysis was carried out to determine any change in the group size of the young resident bulls after the introduction of the older bulls. If the younger resident bulls felt threatened by the older bulls after introduction, they may have formed larger groups during the introduction. These groups may have been expected to return to a group size similar to that prior to introduction once the older bulls had settled into Phinda (e.g. as happened in Pilanesberg, Dickerson 2004). The mean group size of elephant bulls might vary between seasons, with bigger group sizes in the wet, rainy season (Western and Lindsay 1984). For this study, location data from April 2003 to 30 June 2004 were used. Three time periods correlating with three months before the bull introduction (1 April to 30 June 2003), three months after the older bull introduction (1 August to 31 October 2003) and 9-12 months after the older bull introduction (1 April to 30 June 2004) were selected for each individual bull. For this analysis, the number of bulls with each of the five resident bulls most frequently seen (PH1 – aged 36, PH2 – aged 26, PH4 – aged 26, PH6 – aged 24 and PH16 aged 19) and with the three older introduced bulls (PH31, PH32 and PH33) were calculated and compared between the three time periods. In calculating group size, all sightings where a musth bull was present were excluded as the presence of a musth bull behaving aggressively towards other bulls may have influenced the resident bull group sizes. All sightings where bulls were with female breeding herds were also excluded as the presence of a female in oestrus may also have affected the number of bulls present. We analyzed sightings of the new bulls with the resident bulls separately from an analysis excluding all sightings where the older introduced bulls were present.

There was no significant difference in group size between the two three month periods after bull introduction when the new bulls where included in the analysis (T-test: $T = 1.635$, $N = 15$, $P = 0.126$). However when the new, introduced bulls were excluded from the analysis, there was a significant difference between the bull group sizes (ANOVA: $F = 4.084$, $N = 14$, $P = 0.047$). This was driven by the significantly smaller bull group size three months immediately after the introduction of the new bulls when compared to the size prior to introduction (Post Hoc, LSD, $p < 0.05$) and the significant difference between group size prior to introduction and 9-12 months after introduction (Post Hoc, LSD, $p < 0.05$). These results indicate that the significant difference observed between the time periods directly before and after introduction may have been caused by the introduction of the three old bulls rather than a seasonal effect.

In Amboseli, Kenya, bulls' group size seldom averaged more than four individuals (Western and Lindsey 1984), while the mean group size in Tai National Park, Ivory Coast was 2.44 individuals (Merz 1986). The group sizes for the Phinda bulls varied between two to four individuals throughout this analysis. Changes in group sizes took over a year to normalise to a smaller group size in Pilanesberg (Dickerson 2004), whereas the effect in Phinda was much quicker. Introduction of older bulls therefore affected the group sizes in both reserves, and resulted in male group sizes more similar to larger, free-ranging, populations (Dickerson 2004).

Musth duration

In order to determine if the introduction of the three older bulls had any influence on the resident bulls' musth periods, all recordings of bulls in musth between March 2003 and 15 December 2004 were assessed (a total of 12 musth periods were recorded, for 6 different individuals). The musth periods for each individual bull before the introduction of the older bulls were compared with musth periods after the introduction of the older bulls.

Musth was only recorded in 1 out of the 16 resident bulls before the introduction of the older bulls in July 2003. Immediately after the older bull introduction a second young resident bull (PH5) came into musth and stayed in musth for an 87-day period (Table 1). PH5 remained in musth until two days after the first of the older, introduced bulls, PH31, came into musth, two months after being introduced. Both the two other introduced bulls were recorded in musth within eleven months after release, but for short periods.

The oldest resident bull, PH1 was in musth for 159 days during 2004, compared to a musth period of approximately 100 days during 2003. During his musth period in 2004, PH1 was found mainly in the north of the reserve associated with the breeding herds, while the older bulls were primarily utilizing the south of the reserve (Druce et al. 2006b). This difference in area utilization may explain why the older bulls had no influence on PH1's musth periods. As a result, these different groups of bulls would not come into contact with each other.

Both bulls that were resident before the introduction of the three bulls in 2003 (PH1 and PH5), had musth periods at about the same time of the year in both 2003 and 2004. The total musth period of each of the introduced bulls was still less than one third of the time that PH1 was in musth after the introductions.

The introduction of the older bulls appears to have been a success, with all three bulls settling into the reserve and all coming into musth for the first time in their new reserve within the first eleven months after introduction. This was quicker than the bulls that were introduced into Pilanesberg (Slotow and van Dyk 2004). PH31 was the first bull to come into musth, and did so within two months of introduction. This is in contrast to musth periods displayed by older bulls introduced to Pilanesberg National Park. In Pilanesberg, the first older, introduced bull to come into musth, did so only six months after introduction, while one bull still had not come into musth three years after introduction (Slotow and van Dyk 2004). One of the goals of introducing older bulls was to attempt to reduce the abnormally long musth periods of the oldest resident bull in Phinda (PH1). By December 2004, the introduction of the older bulls has had no effect on the musth periods of PH1, with this bull still displaying abnormally long musth periods. Another resident bull (PH5), which had not been recorded as coming into musth prior to the older bull introduction, did so within a month after the introduction and also displayed a long musth period. However, this may not have been the first time that this bull came into musth as monitoring of the Phinda elephant population was only initiated at the beginning of March 2003 and no records of bull musth periods were kept prior to this date.

The older bulls may not have had an influence on the musth periods of the resident bulls, as occurred in Pilanesberg, for a number of reasons. In Pilanesberg, all six bulls that were introduced were older than the resident bulls and as a result would have suppressed the musth behaviour of the younger resident bulls. However, in Phinda, only one introduced bull was older than the oldest resident bulls, with another introduced bull being approximately the same age and the third even younger. While PH1 had been the oldest bull on Phinda prior to the introduction, all three of the introduced bulls came from an elephant population where they were not the oldest bulls and would probably never have displayed musth periods as long as that displayed by PH1 (Poole 1987, Slotow et al. 2000). Their length of musth periods that they displayed after release correlated with musth periods for their age in a normal population (Poole 1987, Slotow et al. 2000). Further research will be needed to determine if the musth periods of the resident bulls falls in line with those displayed by other bulls of those ages in elephant populations with a normal age structure.

With the exception of Pilanesberg National Park (Slotow et al. 2000, Dickerson 2004, Slotow and van Dyk 2004), no studies have been done in small, enclosed reserves to determine the effect and success of older bull introductions into established elephant populations. This study was, therefore, important to monitor and determine if the goals of introduction were accomplished.

The older bulls successfully established themselves into the population. The introduction helped in normalising the age structure, although some of the younger bulls may still need to be removed in order to produce a more normal bull population. In Phinda the resident bull population has remained unchanged until present, although in the Pilanesberg scenario all the problem animals were removed from the reserve (Dickerson 2004). All the introduced bulls in Pilanesberg were older than the resident bull population, while in Phinda only one introduced bull was older then the oldest resident bull. Both these factors appear to have contributed to Pilanesberg's immediate success. Phinda's older bull introduction resulted in no major disruptions to the resident bull behaviour, with only subtle effects on the resident group sizes and grouping behaviour. These results, in combination with those from the Pilanesberg introduction (Slotow and van Dyk 2004), indicate that introduction of older male elephants into small populations does not pose major risks to the behaviour of the introduced or resident elephants.

Table 1. Effect of introducing older bulls on musth in resident Phinda bulls.

Bull	**Musth before introduction**		**Musth after introduction**	
	Dates	**Duration**	**Dates**	**Duration**
PH1	March – 8 April 2003	> 39 days	1 March – 6 August 2004	159 days
	19 June – 19 August 2003[1]	61 days		
PH5	6 August – 31 October 2003	87 days	16 August – 4 November 2004	81 days
PH20	No musth period		27 September – 2 October 2004	6 days
PH31	Introduced in 2003		28 October – 31 November 2003	34 days
			28 October – 27 November 2004	31 days
PH32	Introduced in 2003		9 January – 14 January 2004	6 days
			16 September – 20 October 2004	35 days
PH33	Introduced in 2003		2 June – 10 June 2004	8 days
			31 October 2004 onwards	> 45 days

Note[1]: PH1 went out of musth within 17 days of PH31 being released from the boma

CHAPTER 3

THE EFFECT OF MATURE ELEPHANT BULL INTRODUCTIONS ON RANGING PATTERNS OF RESIDENT BULLS: PHINDA PRIVATE GAME RESERVE, SOUTH AFRICA.

Abstract

Increasing popularity of wildlife viewing has resulted in a rapid increase in small, enclosed reserves in South Africa. The African elephant is one of the many species that has been reintroduced into these reserves for eco-tourism. These elephant populations were established as young (<10 years old) orphans from prior Kruger National Park culling operations. Consequently, this abnormal sex and age structure of these introduced populations has influenced their behavioural and spatial ecology. In Pilanesberg National Park this abnormal behaviour was corrected by introducing older bulls and culling certain problem elephants. In July 2003, three older bulls (29 to 41 years old) were introduced into Phinda Private Game Reserve, KwaZulu-Natal, South Africa in order to normalise the bull age structure. These introduced bulls were monitored intensively after release, as was the resident bull population, both before and after introduction of the older bulls. The introduced bulls settled into restricted ranges separate from the family groups. All the resident bulls decreased their home ranges at first, with most increasing their home ranges a year later. The resident bulls' change in ranging patterns was due more to ecological factors than to the influence of the mature bull introduction. This study indicates that the introduction of older male elephants into small populations does not pose major risks or animal welfare concerns.

Keywords: *Loxodonta africana*, adaptive management, movement patterns, kernel ranges, GIS

Introduction

Wildlife viewing in protected areas as a form of recreation is steadily increasing in popularity. As a result there has been a rapid increase in the number of small reserves (<1000 km^2) during the last few years in South Africa (Druce et al. 2004, Slotow et al. 2005). Although some of these reserves have been developed to enhance biodiversity conservation, most of them exist purely for the eco-tourism industry. Tourism entails the reintroduction of valuable-viewing species into reserves, sometimes regardless of the ecology and the sustainability of these and other species. The African elephant (*Loxodonta africana*) is one of the key species in the ecotourism industry. As a result, many state and private game reserves have reintroduced elephants, many of which were orphaned, surplus elephants originating from culling operations in Kruger National Park (Garaï et al. 2004, Slotow et al. 2005). As these small reserves are enclosed by electric fences which prevent any natural immigration and emigration, they need to be actively managed (Slotow and van Dyk 2004, Slotow et al. 2005) to ensure that elephants can meet all of their ecological and social needs (Garaï et al. 2004).

The basic unit of elephant social organisation is the family group (Laws and Parker 1968, Douglas-Hamilton 1973). Males born into the family group will leave the group or are forcibly ejected after reaching puberty, which is usually between the age of 14 and 17 years (Poole et al. 1984, Poole 1989) Within these bull groups male association is random and they do not form any long-term bonds with other individuals (Laws and Parker 1968, Moss and Poole 1983).

Phinda Private Game Reserve was established in 1991, with an area of approximately 150 km^2 (Fig. 1). The core of Phinda's elephant population was introduced from Kruger National Park between 1992 and 1994. These elephants were orphans from prior Kruger culling operations, and because equipment to transport elephants was limited to animals shorter than 2 m, all the individuals were young and within the same age class (approximately 10 years old or younger at introduction). During 1994 four adult elephants, two bulls and two cows (approximately 20-25 years of age) were introduced from Gonarezhou National Park, Zimbabwe. During June/July 2003 a total of 37 elephants of four different family groups were translocated from Phinda to other reserves. Three older bulls (see below) from Sabi-Sand in Limpopo Province, South Africa were introduced into Phinda between July and August 2003. In July 2004, the total elephant population was 78 individuals, including 19 adult bulls.

Prior to the bull introduction in 2003, Phinda only had one bull 36 years old (bull code PH1) and 15 young bulls aged between 15 and 26 that were independent of the breeding herds. This age structure was unnatural because of the large proportion of young males of approximately the same age. A natural population structure should have individuals spread through the different age groups. Because the oldest resident bull was approximately ten years older than most of the rest of the Phinda bulls, he dominated the other bulls, remaining in musth for long, continuous periods with abnormal displays of aggressive musth behaviour towards other bulls and humans (Druce et al. 2006a). This was possibly due to no competition or conflict with same age or older bulls. As a result, it was decided to introduce three older bulls to create a more natural age structure within the male population, by filling the age gap of bulls older than 25 years. It was expected they would have an influence on the behavioural, social and spatial ecology of the resident population, as according to previous studies (Slotow and van Dyk 2004), African elephants are sensitive to changes in their social structure.

The aims of this study were to determine (1) the effect of the introduction of three older elephant bulls on a young resident bull populations' spatial ecology, by comparing ranging patterns for selected bulls before, during and after the introduction of new bulls and (2) how the three new bulls settled into the reserve, by determining their ranging patterns immediately after release and comparing them to those of the resident bulls.

Methods

This study was undertaken in Phinda Private Game Reserve, KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E) between March 2003 and June 2004. Both the forest and savanna biomes are represented within Phinda. The vegetation type within the forest biome at Phinda is Sand Forest (Low and Rebelo 1996, Type 3), while the savanna biome within Phinda is described by three vegetation types; Sweet Lowveld Bushveld (Low and Rebelo 1996, Type 20), Natal Lowveld Bushveld (Low and Rebelo 1996, Type 26) and Coastal Bushveld-Grassland (Low and Rebelo 1996, Type 23). Phinda has a summer rainfall regime and temperatures range from a minimum of 10 °C in winter to a maximum of 35 °C in summer. One perennial river, the Mzinene River, flows from west to east through the southern section of Phinda. During the rainy season, surface water is extensive and during the dry periods, six dams, distributed throughout the property, are supplied with borehole water.

Bull introductions and monitoring

The first two bulls (PH32 - aged 29 and PH33 - aged 36) were introduced into the electrified Phinda holding boma on 12 July 2003. These bulls remained in the boma until their release on 14 July 2003. A third bull (PH31 - aged 41) was introduced into the boma on 1 August 2003 and broke out on the evening of 2 August 2003. On the evening of 3 August 2003 he broke out of the reserve though an un-electrified gate. The following day he was recaptured, using immobilisation, and returned to the boma for a further four days before being released into the reserve on the 8 August 2003. Before his second release, all gates were electrified and no elephants have since broken out of the reserve.

All independent adult male and adult female elephants on Phinda were identified through unique ear patterns, tusk size and shape as well as any other body characteristics. Identity templates were drawn for each individual elephant, including the three older introduced bulls. Two of these introduced bulls were fitted with GPS collars. These collars download GPS positions at set time intervals and transmit the GPS points to a ground station using GSM cell-phones. These collars were set to download location points every two hours, which were then stored on a master computer.

The Phinda elephant population was monitored daily from a vehicle and at each sighting all elephants were identified using the master identification file. At every sighting date, time, vehicle GPS location, animal distance and bearing from the vehicle, total group size, number of males, females and young, habitat type, name of adult individuals present and behaviour codes were recorded. Most observations were made from a vehicle on the existing road network, due to the difficulty of driving off road in dense woodland, especially in the north of Phinda. With the extensive road network on the reserve, observations was regarded as being sufficient, with a total of 347 sightings for all five resident bulls for the duration of this study period. However, with only two bulls being collared, and located at will, some individual bulls may not have been seen for extended periods. The maximum period that an individual bull was not located was 29 days, but on average, the period between consecutive sightings for an uncollared bull was 3.9 days.

Ranging patterns

In order to determine if the introduction of the three older bulls had any effect on the resident bulls' ranging patterns, sightings data for the five resident bulls most frequently seen (PH1 – age 36, PH2 – age 26, PH4 – age 26, PH6 – age 24 and PH16 – age 19) were compared with that of the two collared, introduced bulls (PH31 and PH32). For this study, location data from 1 April 2003 to 30 June 2004 were used. Three time periods correlating with three months before the bull introduction (1 April to 30 June 2003), three months after the older bull introduction (1 August to 31 October 2003) and 9-12 months after the older bull introduction (1 April to 30

June 2004) were selected for each individual bull. As there may have been a number of locations recorded for a bull on a particular day, only the first location after 6am each day for individual bulls was used in the analysis. The three-month period a year after the bull introduction was used in the analysis as it correlated with the same season as the previous year immediately before introduction. As a result, any confounding factor of season on bull ranging patterns could be accounted for.

The period from June to October 2003 fell within an extremely dry winter, during which a combination of lucerne, *Eragrostis* grass and sugarcane tops were provided at 10 waterholes and at the airstrip on the reserve (Fig. 1). All the artificially provided food resources were positioned at water points. We assumed that the elephants would concentrate at or near these water sources due to the drought, with the result that the addition of artificial food would not have an influence on their movement patterns and corresponding home ranges.

Before analysis, the data set was checked for possible errors or duplicate records. Each sighting record was checked on a master spreadsheet against the map for accuracy, with any outlying GPS points or sightings that did not match the road name description being corrected and/or deleted. Data were processed in Microsoft Excel and imported to ArcView 3.2 (ESRI). The Animal Movement Analysis ArcView extension (Hooge and Eichenlaub 1997) was used in all GIS analyses to estimate the ranges, with the 95% kernel being used as the estimate of home range and the 50% kernel as an estimate of core range (Burt 1943, Worton 1989, Seaman and Powell 1996). A Least Squares Cross-Validation (LSCV) smoothing factor of 1000 m was used throughout all GIS analyses. Separate maps were produced for the various three-month periods for each individual bull.

The core and home ranges of individuals were compared between the three month period before introduction and three months directly after introduction, as well as between the three months before introduction with the same three month period one year later. Only ranges produced from more than 14 sightings were used in the statistical analysis. Seaman et al. (1999) state that kernel home ranges constructed with less than 30 points result in larger home range estimates. However, for our data, there was no significant effect of sample size on home range size (Linear Regression: $F_{1,17} = 0.16$, $p = 0.96$. Data normal: K-S: $p = 0.695$). We also confirmed no significant non-linear relationships. Therefore the kernel analysis was used in this study as a comparison to assess influences specific to this study site and population over this time period. All sample sizes are presented with the ranges to allow readers to make independent assessments of the interpretations, and interpretations are cautious as sample size was relatively small. Percentage overlap in ranges were calculated by overlaying maps of the prior three month period with maps of the later three month period and then dividing the area of overlap by the prior area (multiplied by 100), to give a percentage overlap area.

Results

Ranging patterns

Overall, the five resident bulls' home ranges were concentrated mainly in the north of the reserve (Fig. 2), although they also utilized the central areas in the south. During the months immediately after the introduction of the three bulls, the resident bulls' home ranges became much smaller and concentrated around water sources.

During the three months prior to the introduction of the new bulls and a year after the introduction, PH1, the oldest resident bull, had a large home range (Fig. 2) that covered a large proportion of the reserve. For the three-month period after the introduction of the older bulls (Fig. 2), his home range included areas in the north and south. During all three of these study time periods, PH1 spent an average of 39 days in musth, while for the period immediately after the introduction, PH1 was only in musth for 19 days (Druce et al. 2006a). This may explain why his home ranges differed in size and distribution from that observed for both the other three-month periods, when he was in musth for almost the entire period. During musth periods, PH1 was mainly seen following breeding herds which tended to move throughout the reserve and have large home ranges (unpublished data). During times when PH1 was not in musth, he was on his own and did not follow herds.

The resident bulls decreased their home ranges (95% kernel) significantly immediately after the introduction of the older bulls (Wilcoxon Signed Ranks, $T = -2.023$, $N = 5$, $p = 0.043$, Table 1). All core (50% kernel) ranges, with the exception of PH6, decreased following the introduction of the older bulls, although this was not significant (Wilcoxon Signed Ranks, $T = -1.214$, $N = 5$, $p = 0.225$). There was a significant increase in both core ranges (Wilcoxon Signed Ranks, $T = -2.02$, $N = 5$, $p = 0.043$) and home ranges (Wilcoxon Signed Ranks, $T = -2.02$, $N = 5$, $p = 0.043$) between the three-month period before the bull introductions with the three month period 9-12 months later (Table 1). We assessed range shift by contrasting overlap of ranges relative to the period before the introduction. There was no significant difference in the overlap of the home (Wilcoxon Signed ranks: $T = -0.674$, $N = 5$, $p = 0.50$) or core ($T = -1.753$, $N = 5$, $p = 0.080$) ranges in the three months after introduction versus 9-12 months after introduction (Table 1).

The two introduced bulls utilized areas on the reserve not frequently utilized by the resident bulls. The oldest bull, PH31, patrolled the western boundary for the duration of the first three months (Fig. 2). The second introduced bull, PH32, had a home range covering most of the reserve during the three-month periods after introduction (Fig. 2). During the first three months after introduction, PH32 had two core ranges, one in the north and the other in the south. A year later, his core range had shifted to the far southern corner of the reserve (unpublished data). The third uncollared introduced bull (PH33) was not used in this analysis, but observational data shows that he associated closely with PH31, the oldest introduced bull (unpublished data). Although these two bulls were introduced on different dates into the reserve, they joined up to form a bull coalition and were only seen apart during each other's musth periods.

Table 1. Effect of bull introductions on ranging patterns of resident bulls and changes in ranging patterns of introduced bulls.

	% overlap of range 3 months after introduction with range 3 months before introduction		**Range change**		**% overlap of range 9-12 months after introduction with range 3 months before introduction**		**Range change**	
Bull	**Core[a]**	**Home[b]**	**Core**	**Home**	**Core**	**Home**	**Core**	**Home**
PH1	33	28	Decreased	Decreased	6	81	Increased	Increased
PH2	75	31	Decreased	Decreased	14	54	Increased	Increased
PH4	31	33	Decreased	Decreased	44	75	Increased	Increased
PH6	36	46	Increased	Decreased	35	43	Increased	Increased
PH16	83	35	Decreased	Decreased	30	68	Increased	Increased

[a]Core = 50% kernel

[b]Home = 95% kernel

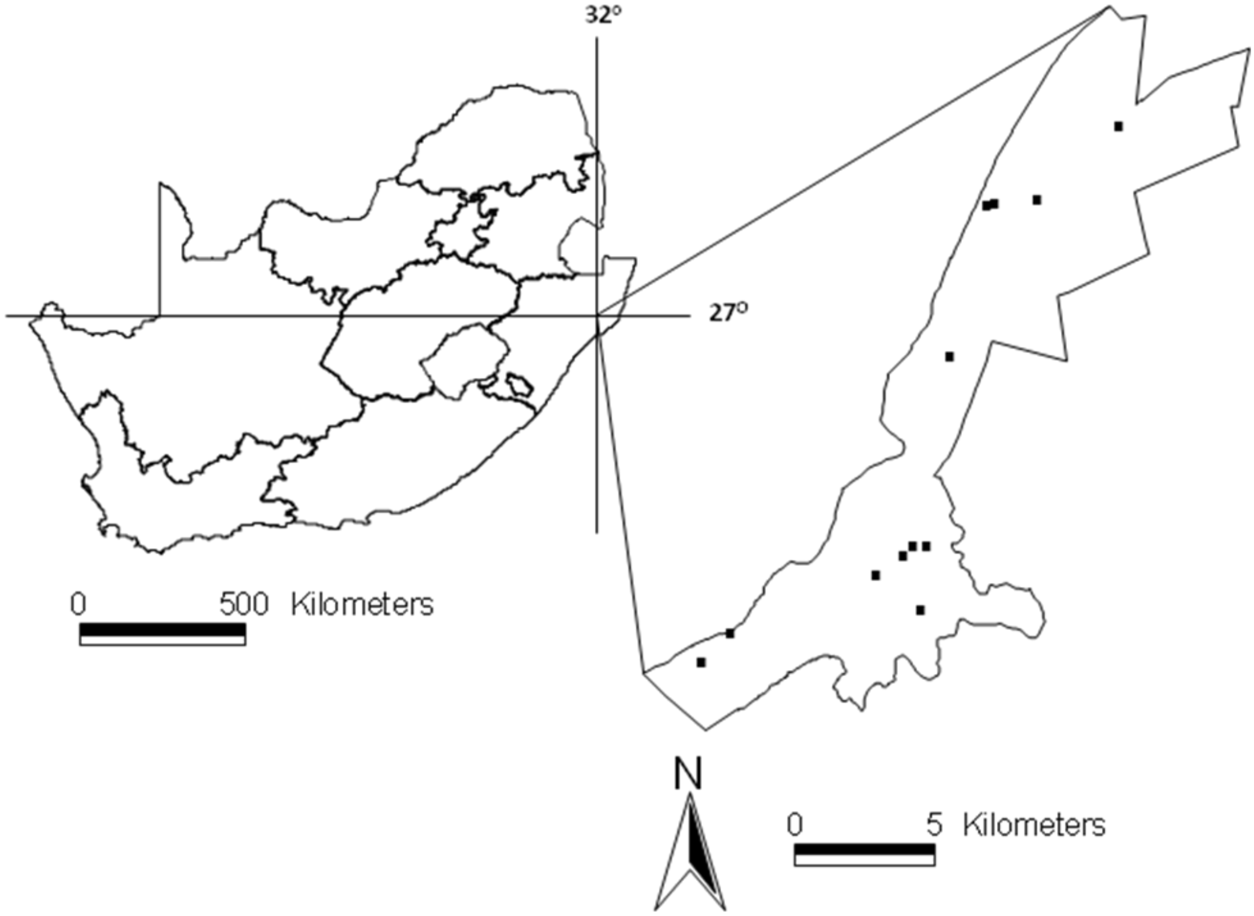

Figure 1. Phinda Private Game Reserve. Black dots indicate the position of sites where artificial feed was provided during the winter of 2003.

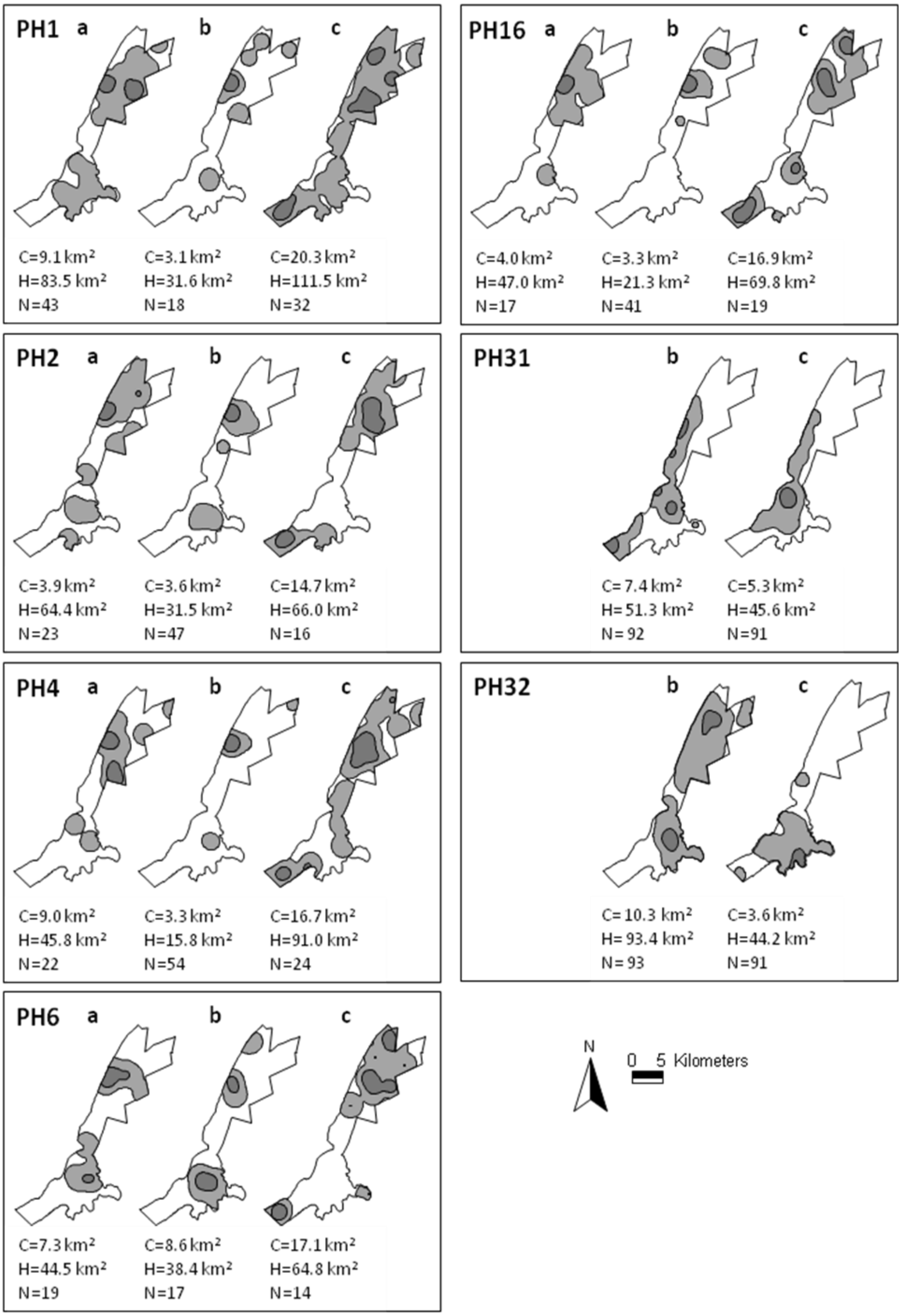

Figure 2. Ranging of bull elephants on Phinda: The effect of the introduction of older elephant bulls on the ranging behaviour of younger, resident bulls. Three maps are shown for each resident bull and two for the introduced bulls: (a) three months before the introduction of the new bulls, (b) three months directly after introduction, (c) three month period 9-12 months after introduction. C = Core ranges (50% kernel **-** dark grey shading) and H = home ranges (95% kernel **-** light grey shading). N = number of sightings used to calculate ranges for that period.

Discussion

With the exception of Pilanesberg National Park (Slotow et al. 2000, Slotow and van Dyk 2001, Dickerson 2004, Slotow and van Dyk 2004), no studies have been done in small, enclosed reserves to determine the effect and success of older bull introductions into established elephant populations. This study was, therefore, important to determine the success of the introduction of the older bulls to Phinda, their effect on the ranging patterns of the resident bulls and to allow comparison with the only other similar study that had been previously undertaken.

The Phinda elephant bulls used relatively small home ranges that varied between 15.8 km^2 and 111.5 km^2. These range sizes are similar to the documented (24 to 139 km^2) range sizes for bulls in Pilanesberg National Park (Slotow and van Dyk 2004), Lake Manyara (14 to 52 km^2 – Douglas-Hamilton 1973) and the Zambezi Valley (156 km^2 –Dunham 1986), but much smaller than male home ranges (157 to 465 km^2) in Kruger National Park (de Villiers and Kok 1997, Hall-Martin 1987). The ranges observed in Phinda are also comparable to the elephant camp within Addo Elephant National Park (area = 103km^2), where the bulls' mean 100% kernel range is 52.8 km^2 (Whitehouse and Schoeman 2003). Thouless (1996) suggests that range size is correlated with rainfall, with smaller ranges at higher rainfall. Shannon et al. (2006) also suggested that in Pongola Game Reserve (fenced area = 73.6 km^2) the home ranges of bulls increase during the dry season. However, in some populations, elephants' home ranges are in the 1000s km (e.g. Leggett 2006, Leuthold and Sale 1973, Lindeque and Lindeque 1991).

The decrease in the resident bulls home ranges during the three-month period immediately after the introduction, may be due to a seasonal influence rather than the introduction *per se*. The resident bull home ranges were concentrated around water resources for this three-month period as it fell within an extremely dry winter. The newly introduced bulls showed larger home ranges during this three-month period immediately after their release. These larger home ranges can possibly be explained as exploration of their new area (similar to findings in Pilanesberg: Slotow and van Dyk 2004). However, it is interesting that the core ranges for the older introduced bulls during the three-month period immediately after introduction was also concentrated around water sources. The resident bulls knowledge of local resource distribution might have been a reason why they did not link up with the older bulls during the introduction period.

Seasonal factors surely seemed to have affected the resident bulls home ranges more than the introduction of the older bulls. Interestingly enough, all the resident bulls avoided the older introduced bulls' core ranges completely and showed only a small overlap with introduced bulls' home ranges. Therefore, the introduction of the older bulls could have influenced the resident bulls in that they avoided the older new bulls. However, the older introduced bulls may also have used spatially separate areas to other elephants, in setting up independent bull areas away from the female family groups.

The introduction of older bulls into the Phinda elephant population helped in normalising the age structure (Slotow et al. 2005), although some of the younger bulls will still need to be removed in order to produce a more normal bull population structure. In Phinda the resident bull population has remained unchanged until present, although in Pilanesberg all the problem animals were removed from the reserve (Slotow et al. 2000, Dickerson 2004). All the introduced bulls in Pilanesberg were older then the resident bull population, while in Phinda only one introduced bull was older then the oldest resident bull. Both these factors appear to have contributed to Pilanesberg's immediate success. The introduction of older bulls into Phinda resulted in no major disruptions to the resident bull behaviour, with only subtle effects on the resident bulls' ranging patterns. The resident bulls' ranging changes responded more to ecological factors than to the influence of the mature bull introduction. These results, in combination with those from the Pilanesberg introduction (Slotow and van Dyk 2004), indicate that the introduction of older male elephants into small populations does not pose major risks to the behaviour of the introduced or resident elephants.

CHAPTER 4
THE RESPONSE OF AN ELEPHANT POPULATION TO CONSERVATION AREA EXPANSION: PHINDA PRIVATE GAME RESERVE, SOUTH AFRICA.

Abstract

Continuous human population expansion pressure on conservation ecosystems restricts wildlife areas, and necessitates active management. In areas of changing land-use and increasing human-animal conflict, responses of wildlife to direct human interventions can inform managers and planners. During August 2004, the boundary fences between Phinda Private Game Reserve and two neighbouring reserves were removed. This study examined behavioural responses of the resident elephants. Older, recently introduced bulls moved into the new area during the first month after fence removal, while younger resident bulls and family groups took between five to eight months. Initially family groups only moved into the new area at night and spent minimal time there, while older bulls spent longer periods of time, regardless of time of day. One year after fence removal, most of the elephants had only expanded their home ranges slightly into the new area. One of the findings of this study is that elephants appear to act cautiously in exploring new areas and responded by moving into the area slowly and over a relatively long time period. This cautious behaviour reduced through time as animals became more familiar with the area. The spatial scale of response of the elephants was relatively small, while the temporal scale of response was relatively large.

Keywords: *Loxodonta africana*, ranging behaviour, reaction time, cautious behaviour, response indicator, GIS.

Introduction

The continuous decline and fragmenting of ecosystems through increased pressure by human expansion (Bissonette and Adair 2008) often results in conservation ecosystem that are small, isolated and fenced. This restricts wildlife populations and can result in local overpopulation of a particular species, amongst other problems (van Aarde and Jackson 2007). The continuous loss of habitat emphasizes the importance of ecosystem conservation and the understanding of how wildlife uses ecosystems (Douglas-Hamilton et al. 2005). Many studies have shown that animals adapt their ranging and foraging behaviour, or their daily movement rhythms, to avoid human-induced disturbance and unexplored or unknown areas (Douglas-Hamilton et al. 2005, Maude 2005, Aleper and Moe 2006, Burke et al. 2008). Once a conservation area is expanded, the response of wildlife can give wildlife managers and conservation planners good insight into these animals' welfare and their perception of both the existing and new area (Osborn and Parker 2003, Boone and Hobbs 2004, Douglas-Hamilton et al. 2005).

The African elephant (*Loxodonta africana* L.) is a species that has been extensively studied, but clear management answers and solutions are lacking. It is still one of the most difficult species to manage (Hoare 2001) as it has the potential to threaten biodiversity (Western 1989, van Aarde et al. 1999, Kerley et al. 2008). Its longevity, successful reproduction and limited natural enemies, ensure that populations grow rapidly throughout southern Africa (Bengis 1996, Slotow et al. 2005, Mackey et al. 2006).

Within South Africa, approximately 80 elephant populations occur within small (<1000 km^2), enclosed reserves (Slotow and van Dyk, 2001, 2004; Whitehouse and Schoeman 2003, Garai et al. 2004). Within these enclosed populations natural immigration or emigration are prevented (Novellie et al. 1991), with the result that most reserves that are suitable to hold elephants already face problems with perceived overpopulation (Owen-Smith et al. 2006). While many options are being considered to alleviate population pressures, range expansion and linkages is attractive as an ethical, long-term solution (see Biggs et al. 2008).

This study was conducted within the Munyawana Conservancy (185 km^2), KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E). This conservancy was formed in August 2004 when boundary fences between Phinda (area 150 km^2, established 1991) and two neighbouring reserves, Zuka and Mziki Pumalanga, were removed, with a resultant 23% increase in size (Fig. 1).

Little is known about the response of wildlife, especially elephant populations, to the removal of original boundary fences and the inclusion of new areas of land. A knowledge of the response of wildlife to such changes can be valuable to reserve managers by informing decision making. The objective of this study was to determine the temporal and spatial response of elephants to range expansion, through boundary fence removal. To achieve this we determined: (1) how long it took before the elephants moved into the new area, as well as the greatest distance elephants moved from the old fence line into the new area within a one-year period after fence-removal; (2) what time of day the elephants preferred to move into the new area; (3) the influence of the fence removal on the elephants' ranging patterns; and (4) if there were any differences in movement rates of elephants within the old verses the new area after the boundary fences were removed.

Methods

The study was undertaken between July 2003 and September 2005. The study area consists of a mosaic of different savanna woodland type and Sand Forest, has a summer rainfall regime, and temperatures range from 10 °C in winter to 35 °C in summer. Water, through artificial provisioning, is widespread through the reserve and does not limit elephant movement. The reserve is surrounded by an electrified boundary fence.

The Phinda elephant population was introduced between 1992 and 1994 (54 orphans from culling operations plus four adult elephants), with an additional three mature adult bulls in 2003. By 2003 the population had reached 110, and in June/July 2003 37 elephants in four different family groups were translocated from Phinda. In July 2005 the population was 81 individuals, consisting of 19 independent adult bulls and five family groups. Zuka also contained a small group of 4 young elephants (<7 years old when introduced in 1996). Phinda's active adaptive elephant management (sensu Biggs et al. 2008) was mainly driven by the fast population growth rate and the possible impact a high density of elephants may have had on the environment, especially within the Sand Forest (Slotow et al. 2004).

Monitoring

The Phinda elephant population has been monitored daily since March 2003. All adult male and female elephants were identified through unique characteristics. One female of the young Zuka group was identified (the other three individuals were never clearly seen). The Zuka group remained within their established ranging area in the mountain valleys of Zuka, never associated with the Phinda population and were excluded from analyses.

The Munyawana Conservancy contains a good network of roads, which are patrolled daily by security staff and field guides. Elephant sightings were called in via radio and the monitoring team relocated the elephants to record data. This ensured an accurate recording of the Phinda elephant population’s first movements into the new area. These security staff and field guides drove random routes throughout the reserve, resulting in no particular bias in location data. In addition, we used radio telemetry to locate collared elephants. Two of the older adult males introduced in 2003, and an adult female within each of the five family groups were collared (see Table 1 for collared individuals and dates collars were fitted) with GPS/GSM or GPS/satellite collars. The latter were set to download location points at least every 6 h (two day-time points and two night-time points), while GSM collars downloaded every two hours. Both observed sightings location data and collar location data were used in analyses. Female elephant collar data represented locations for her entire family group, while the male collar data represented only that individual.

At each sighting, all elephants were identified using the master identification file. We recorded the date, time, vehicle GPS location, animal distance and bearing from the vehicle, total group size, number of males, females and young, habitat type, name of adult individuals present and behaviour codes. For analytical purposes, we separated the recently introduced bulls from the resident (originally introduced) bulls, as the new bulls were older than the resident bulls and tended to behave differently.

Time taken to move into new area

Prior to fence removal, sightings of elephants were recorded throughout the reserve, although the intensity and seasonal utilisation by elephants greatly varied throughout the reserve (Druce et al. 2006b, Repton 2007). The recently introduced bulls were often sighted along the western boundary, while the breeding herds were only occasionally seen along this boundary. None of the animals appeared to actively avoid walking along the fences and for some time after the boundary fence removal elephants (mainly female family groups) were observed to continue to respect the fence area as though the old fence was still in place and did not attempt to cross into the new area.

Prior to the boundary fence removal, Phinda was approximately 30 km long and varied from 1.4 km to 9 km wide (Fig. 1). The inclusion of the new area resulted in a 23% increase in area, and was strategically positioned directly west of the narrow central corridor, which widened to between 3.4 km and 9 km (Fig. 1).

Location data of the individual bulls and family groups for the 13 month period after fence removal (1 September 2004 to 30 September 2005) were imported into ArcView 3.2 (ESRI). We determined how long it took the elephants to move into the new area by clipping the data for the expanded area, and sorting by date. We measured the shortest and maximum distance from the first recorded GPS point within the new area for a bull or group to the old boundary using the measuring tool in ArcView 3.2, and noted the date of the maximum distance.

These analyses were done using the five individual family groups (family herd codes: FH1, FH2, FH3, FH4 & FH5), the three introduced bulls (estimated ages in January 2006 in parentheses: IM1 (43), IM2 (31) & IM3 (38)) and five resident bulls most frequently seen (RM1 (38), RM2 (28), RM3 (28), RM4 (26) & RM5 (21)). All the study animals used in this analysis move independently of each of the other study animals; however, for short periods of time these family groups or independent bulls joined-up randomly. Therefore, we considered each male or family group independent from the rest.

We assessed elephant movements for each study animal the day before and the day after their first entry into the new area using the ArcView Animal Movement Analysis extension (Hooge and Eichenlaub 1997). We determined the direction of movement by creating poly-lines from point-files. When direct lines crossed a boundary fence, we manipulated them to follow the shortest line along the boundary.

Preferred time of day spent in new area

We determined if there was a preferred time of day that the five individual family groups, the three introduced bulls and the five resident bulls most frequently seen moved into the new area. For each individual, we contrasted the number of occasions that they were located in the new area during day-time (6am to 6pm) versus night-time (6pm to 6am) using a Paired-Sample T-test in SPSS (11). Data were normal (Kolmogorov-Smirnov Test: $p > 0.05$). Because of sexual segregation in elephants (Stokke and du Toit 2000, 2002; Shannon et al. 2006, Shannon et al. 2008), we repeated this analysis using only the data for the five family groups.

Number of consecutive days spent in new area

Duration of time spent in the new area was assessed by counting the number of consecutive days when elephants had been in the new area for at least 48 h. When two or more consecutive days were spent in the new area, we counted the sum of days, the maximum and minimum duration, and the number of separate occurrences of consecutive days.

Movement patterns

We assessed the effect of the removal of the boundary fence and the inclusion of new land on ranging patterns of the five family groups, the three introduced bulls and the five resident bulls most frequently seen. We used a before-after contrast, using the same period in the year (to remove confounding effects of season): 13 months before the fences were removed (1 July 2003 to 31 July 2004) and 13 months after fence removal (1 September 2004 to 30 September 2005). We used two locations per day, at approximately 08:00 h and 16:00 h.

We equalised sample sizes across time periods for each focal animal to reduce bias. We used Hawths tools in ArcGIS 8.3 (ESRI) to randomly select sub-samples from the data set with the larger sample size, which was equal to that of the smaller sample size. We estimated the 95% kernel (used as the estimate of the home range) and the 50% kernel (an estimate of core range) (Burt 1943, Worton 1989, Seaman and Powell 1996) using the ArcView Movement Analysis extension (Hooge and Eichenlaub 1997). A Least Squares Cross-Validation (LSCV) smoothing factor of 1000 m (this was the mean for all the data during preliminary data analysis) and an Output Grid Cell Size of 100 m were used throughout. Separate maps were produced for both time periods for each study group.

We calculated shifts in ranging by overlaying either core or home range maps of the prior 13 month period with maps of the later 13 month period and then dividing the area of the overlap by the prior area (multiplied by 100) to give a percentage area overlap. Overlaps were contrasted using Paired-sample T-tests in SYSTAT (10) (Data were normal: Kolmogorov-Smirnov Test: $p > 0.05$).

Movement rates

We contrasted movement rates for the five family groups (FH1, FH2, FH3, FH4 & FH5) and the two collared introduced bulls (IM1 & IM2) using collar data only. We determined daily movement by calculating the straight-line distance between two points on subsequent days that were 12 h apart using the Animal Movement extension in ArcView 3.2. This was converted to km/h, and the rates within the original Phinda area were contrasted with the rates within the expanded area using a T-test after square root transformation to normalise data (Kolmogorov-Smirnov Test: $P > 0.05$) in SPSS (11) (graphs were produced using the untransformed raw data). While this did not provide an exact rate of movement due to the coarse nature of the data, i.e. we could not detect finer movements such as backtracking, the technique was consistent across individuals, and thus provided an index by which we could compare among the two areas.

Results

Time taken to move into new area

The first elephants recorded crossing into the new area were the introduced bulls (IM1 and IM2), which moved in within one month after the fence removal. During the second month after the fence removal, the first of the resident bulls (RM4) crossed the old boundary, with the rest of the resident bulls only crossing five to eight months later. The first family group (FH4) only crossed into the new area four months after fence removal, while the rest of the family groups (a total of 67% of the Phinda elephant population) took between six to eight months before entering the new area for the first time.

The first locations recorded within the new area were only at a distance of approximately 8 to 108 m from the old boundary and were for the two introduced bulls, IM1 and IM2 (Table 2). One family group (FH5) moved a maximum distance of 2.5 km from the boundary when they first crossed into the new area, while the rest of the female groups only moved a maximum distance of between 250 m to 850 m from the old boundary when they first crossed into the new area. All the first locations recorded for the resident bulls within the new area were less than one kilometre from the old boundary.

The maximum distance (approximately 5.7 km) moved into the new area from the old boundary was for the introduced bull, IM1 and was recorded within the first month after the fence removal (Table 2). The family group FH5 took six months, while the rest of the family groups took between 11 and 12 months before their greatest distances from the old boundary were recorded. It took the resident bulls 2 to 8 months before their greatest distances from the old boundary were recorded. The shortest maximum distance from the farthest location point in the new area to the old boundary (<1 km) was recorded for a resident bull (RM5), while the five family groups' maximum distances moved from the old boundary varied between 1.3 km and 5.5 km (Table 2).

Before elephants first entered into the new area, they were often moving along the old boundary before they crossed in (Fig. 2). Some elephants used the new area as a short-cut, avoiding the previously narrow bottle-neck area (example is FH1 in Fig. 2). Interestingly, the first time most of the elephants moved into the new area, they only went a short distance from the old fence and spent minimal time (mostly less than 12 h) before moving out again. All the elephant groups were seen in Phinda the day before their first recorded entry into the new area, except for three of the resident bulls (RM1, RM3 & RM4).

Preferred time of day spent in new area

The introduced bulls and the five family groups spent time during both day and night in the new area, while the resident bulls were only seen during the day in the new area (Table 3). There was no significant difference (T-test, $t = -1.151$, $N = 13$, $P = 0.272$) between the number of times animals were recorded in the new area during the day and night time periods for all the studied groups. When analysed separately, the family groups spent significantly more time in the new area during night time (T-test, $t = -2.847$, $N = 5$, $P = 0.047$).

Number of consecutive days spent in new area

Elephants generally spent less than 24 h within the new area within the first year after fence removal. Family group FH2 spent the longest period in the new area. This was 13 consecutive days (Table 3), 11 months after fence removal. Two family groups (FH1 and FH5) never spent longer than 24 h in the new area within the first year after the fence removal.

Movement patterns

All the family groups, the oldest resident bull (RM1) and all the introduced bulls used most of the reserve as their home range during the period before the fence removal, with multiple core ranges spread throughout Phinda (Fig. 3 & 4). However, the resident bulls' home ranges were much smaller than the reserve area and consisted only of small core ranges which were mainly concentrated in the north of the reserve. The majority of groups and individuals used in this analysis, only expanded their home ranges slightly into the new area during the year after fence removal. Before fence removal, all individuals and groups' home ranges varied from 59.2 km^2 – 135.4 km^2, while after fence removal these home ranges varied from 52.8 km^2 – 159.5 km^2. All the home ranges increased after fence removal, except for one family group (FH5), a single resident bull (RM4) and two introduced bulls (IM1 and IM3).

In the year period before fence removal, all five family groups had large home ranges with core ranges' in both the north and the south of the reserve, except for family group FH1, which only had a core range in the north of the reserve (Fig. 3). After fence removal, three family groups (FH1, FH4 and FH5) kept their home ranges mainly within the old Phinda property and only expanded slightly across the old boundary, while four of the family groups (FH1, FH3, FH4 and FH5) had no core ranges within the new area. The fifth family group (FH2) expanded their home range extensively into the new area, resulting in their home range covering most of the Munyawana Conservancy (Fig. 3). They were the only group to establish a core range within the new area.

During the period before fence removal, all the resident bulls had small, scattered home ranges, which were much smaller than the reserve area. After fence removal, all these resident bulls continued to have small, scattered home ranges, and only slightly expanded into the new area (Fig. 4). The resident bull (RM3) was the only individual whose home range did not include part of the new area after the fences were removed. The oldest resident bull (RM1) showed similar ranging patterns to the older, recently introduced bulls, both before and after the fence removal. Before fence removal, all four older bulls' (RM1, IM1, IM2 and IM3) home ranges included most of the property, with three bulls' (RM1, IM1 and IM3) home ranges concentrated along the western boundary (Fig. 4). During the period after fence removal, one introduced bull (IM2) increased his home range size and ranged extensively throughout the new area, while all three other old bulls (RM1, IM1 and IM3) had home ranges, which only extended partly into the new area. The two introduced bulls (IM1 and IM2) and the oldest resident bull (RM1) were the only bulls to establish core ranges within the new area.

There was no significant change in the home ranges (95% kernel) before and after the fence removal (T-test, $t = -1.231$, $N = 13$, $P = 0.242$). All family groups had a 82-98% home range overlap between the period before with the period after fence removal. The bulls tended to have less home range overlap (range: 30-98%). There was no significant difference in the core range (50% kernel) before and after boundary removal (T-test, $t = 1.924$, $N = 13$, $P = 0.078$) (Table 4). Only one family group (FH2) and the two recently introduced bulls (IM1 and IM2) moved to the farthest western boundary of the new area.

Overall, the Phinda elephant population had extensive home ranges throughout the original reserve before the fences were removed. Subsequent to the boundary fence removal, an increase in home range size and expansion of ranges of elephants into the new area was gradual and diminutive. Thirteen months after fence removal, only three groups (family group FH2 and the introduced bulls IM1 and IM2) were found to have expanded core ranges into the new area.

Movement rates

The movement rates for the elephants when in Phinda were significantly faster than those in the new area (T-test, $t = 4.001$, $N = 694$, $P < 0.001$). The average calculated movement rate within Phinda was slightly below 0.14 km/h, while the movement rates in Zuka were on average 0.09 km/h (Fig. 5 (b)). Movement rates were calculated for all individuals or groups at the earliest time after fence removal where they spent more than two consecutive days in the new area. For the two recently introduced bulls this was less than a month after the fence removal, while for the three family groups (FH2, FH3 & FH4) that spent more than two consecutive days in the new area this only occurred between 7-12 months after the fence removal.

Table 1. Collared elephant individuals and their collar information.

Collared Elephant ID	**Sex**	**Herd or Bull Code**	**Date – collar fitted**	**Date – collar removal [1]**	**Collar Type**
PH31	bull	IM1	5 Aug 2003	3 Nov 2004	GSM cell
PH32	bull	IM2	12 Jul 2003	17 Jan 2005	GSM cell
PH39	cow	FH5	20 Oct 2003	18 Apr 2004	GSM cell
PH39	cow	FH5	18 Apr 2004	Still on	GSM cell
PH23	cow	FH1	15 Jul 2004	Still on	Satellite
PH42	cow	FH1	16 Jul 2004	16 Jun 2005	Satellite
PH36	cow	FH4	20 Jul 2004	16 Jun 2005	Satellite
PH27	cow	FH4	20 Jul 2004	Still on	Satellite
PH44	cow	FH2	16 Jun 2005	Still on	Satellite
PH30	cow	FH3	16 Jun 2005	Still on	Satellite

Note: [1]PH32’s collar came off naturally, while all other collars were fitted and removed by Phinda management.

Table 2. The time taken for the elephant family groups and bulls to move into the new area, with the first recorded date, as well as the date recorded for the maximum distance from the old boundary.

Family herd or Bull codes	Date of first crossing into new area	Time from fence removal to first entry into new area	Maximum distance from old boundary on first entry into new area	Date of greatest distance moved from old boundary	Duration of time before greatest distance moved	Maximum distance from old boundary
Family Herds						
FH1	05/02/2005	6 months	250 m	27/07/2005	11 months	2504 m
FH2	02/04/2005	8 months	843 m	04/08/2005	12 months	5490 m
FH3	02/04/2005	8 months	248 m	13/08/2005	12 months	1290 m
FH4	05/12/2004	4 months	270 m	13/08/2005	12 months	4220 m
FH5	14/02/2005	6 months	2510 m	14/02/2005	6 months	2510 m
Resident Bulls						
RM1	02/04/2005	8 months	722 m	03/04/2005	8months	722 m
RM2	25/02/2005	6 months	473 m	25/02/2005	6 months	473 m
RM3	11/03/2005	7 months	15 m	02/04/2005	8 months	870 m
RM4	31/10/2004	2 months	320 m	31/10/2004	2 months	320 m
RM5	15/01/2005	5 months	97 m	15/01/2005	5 months	97 m
Introduced Bulls						
IM1	26/08/2004	1 month	108 m	12/09/2004	1 month	5680 m
IM2	26/08/2004	1 month	8 m	14/11/2004	3 months	4048 m
IM3	31/10/2004	2 months	320 m	29/04/2005	8 months	1778 m

Table 3. Preferred time of day spent by elephants in the new area, with the number of occasions elephant family groups or bulls were recorded. Day refers to 6am to 6pm, while night refers to 6pm through to 6am.

Family herd or Bull codes	Total number of sightings for the time period[1]	Total number of sightings in the new area for the time period[1]	Sightings in the new area for the time period[1]		Consecutive days in the new area during the 12 month period after fence removal		
Family Herds			Day	Night	Total number of consecutive days	Range of days[2]	Number of occurrences of consecutive days
FH1	731	27	5	22	0	-	0
FH2	304	68	33	35	27	5-13 days	3
FH3	307	33	14	19	4	4 days	1
FH4	643	35	9	26	2	2 days	1
FH5	339	13	4	9	0	-	0
Resident Bulls							
RM1	27	1	1	~[3]	~	~	~
RM2	58	1	1	~	~	~	~
RM3	110	2	2	~	~	~	~
RM4	40	4	4	~	~	~	~
RM5	39	1	1	~	~	~	~
Introduced Bulls							
IM1	101	49	24	25	20	2-7 days	4
IM2	308	78	42	36	26	2-8 days	5
IM3	44	4	3	1	0	-	0

Note: [1]Time period, 13 months after fence removal (1 September 2004 to 30 September 2005).

[2]Minimum to maximum number of consecutive days elephants spent within the new area.

[3]The night-time movement of the resident bulls are unknown (no collared individuals).

Table 4. The effect of fence removal on the core and home ranges of the elephant population.

Family herd or Bull codes	% overlap of range 13 months after fence removal with range 13 months before fence removal		Range change	
	Core[1]	Home[2]	Core	Home
Family Herds				
FH1	52	98	Increased	Increased
FH2	33	82	Decreased	Increased
FH3	27	96	Decreased	Increased
FH4	44	94	Decreased	Increased
FH5	25	95	Decreased	Decreased
Resident Bulls				
RM1	0	73	Decreased	Increased
RM2	28	70	Decreased	Increased
RM3	100	98	Increased	Increased
RM4	10	59	Decreased	Decreased
RM5	0	70	Decreased	Increased
Introduction Bulls				
IM1	16	48	Decreased	Decreased
IM2	37	91	Decreased	Increased
IM3	0	30	Decreased	Decreased

Note: [1]Core = 50% kernel

[2]Home = 95% kernel

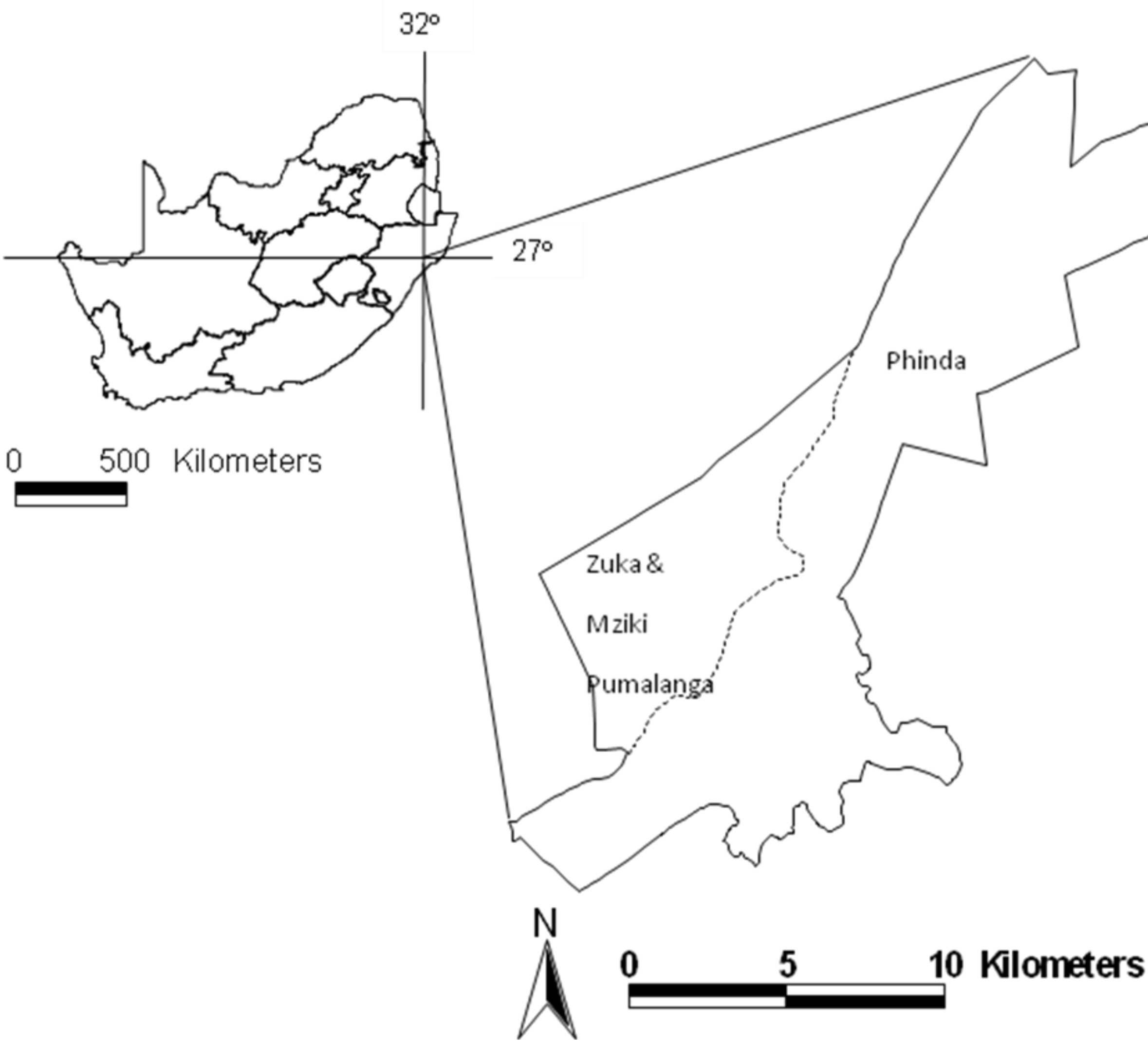

Figure 1. Munyawana Conservancy. The dashed line indicates the position of the boundary fence between Phinda and the new sections of Zuka, and Mziki Pumalanga before the fences were removed during August 2004.

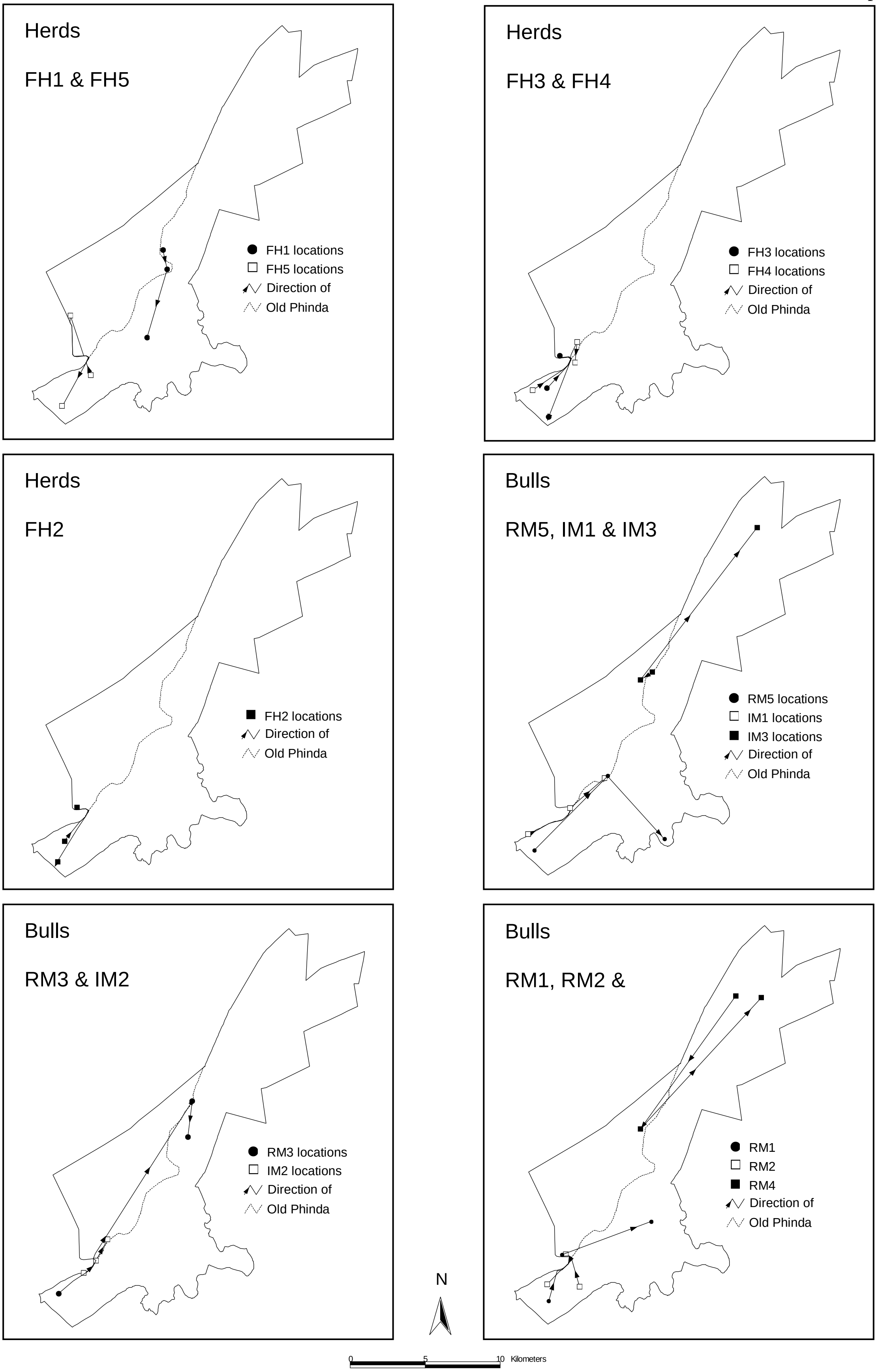

Figure 2. Movement of Phinda elephants on their first entry into the new section, shown on combined maps. The location immediately before and after the first entry location are indicated and connected with a directional line of movement. Where the direct connective line between two location points crossed out of the existing boundaries, the line was adjusted to follow the boundary.

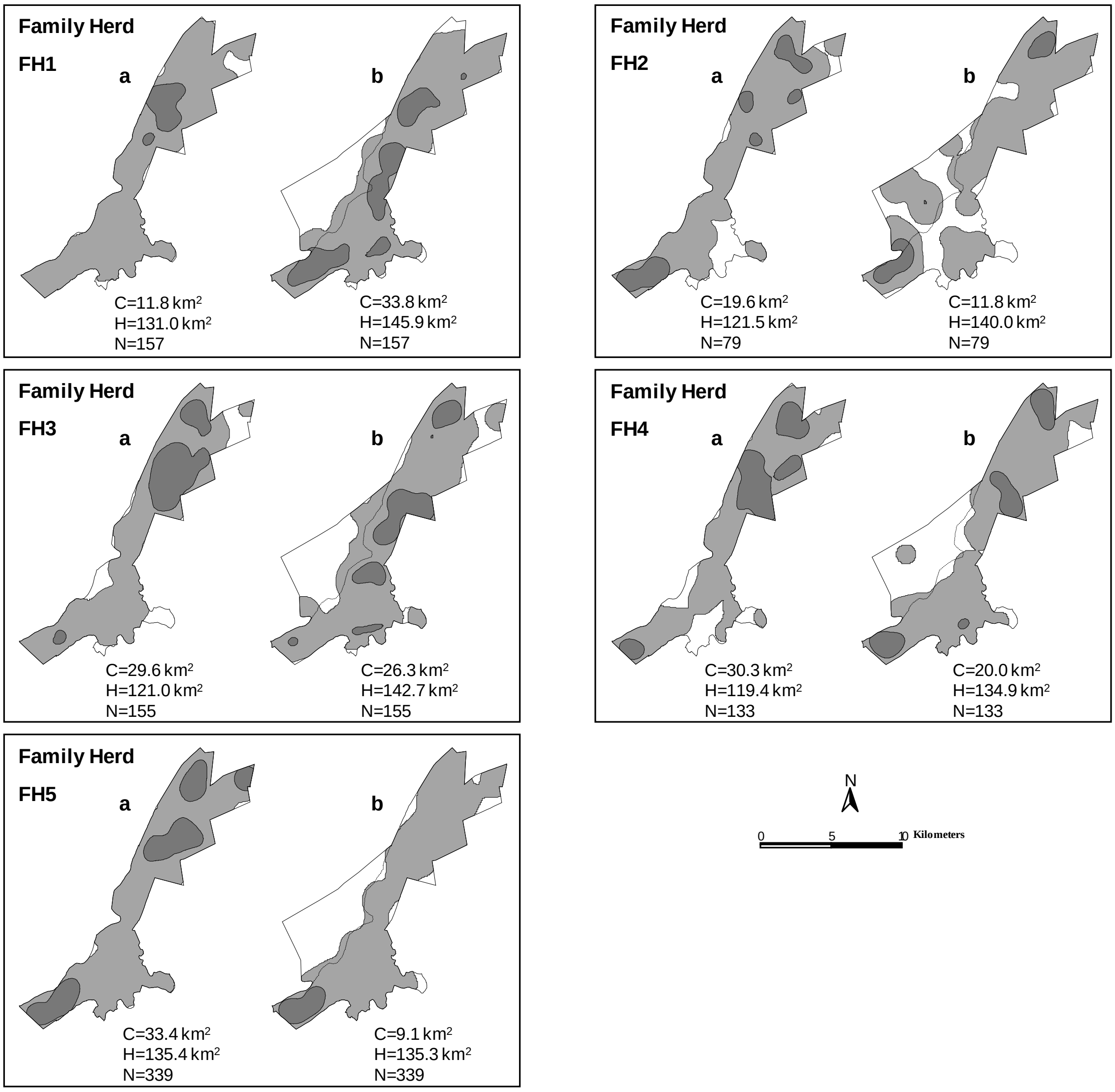

Figure 3. Ranging of the Phinda elephant female family groups on Munyawana Conservancy: The effect of the fence removal on the ranging behaviour of the family herds. Two maps are shown for each family group: **(a)** the 13 month period before the fence removal, **(b)** the 13 month period directly after the fence removal. C = Core ranges (50% kernel – dark grey shading) and H = Home ranges (95% kernel – light grey shading). N = number of locations used to calculate ranges for that period.

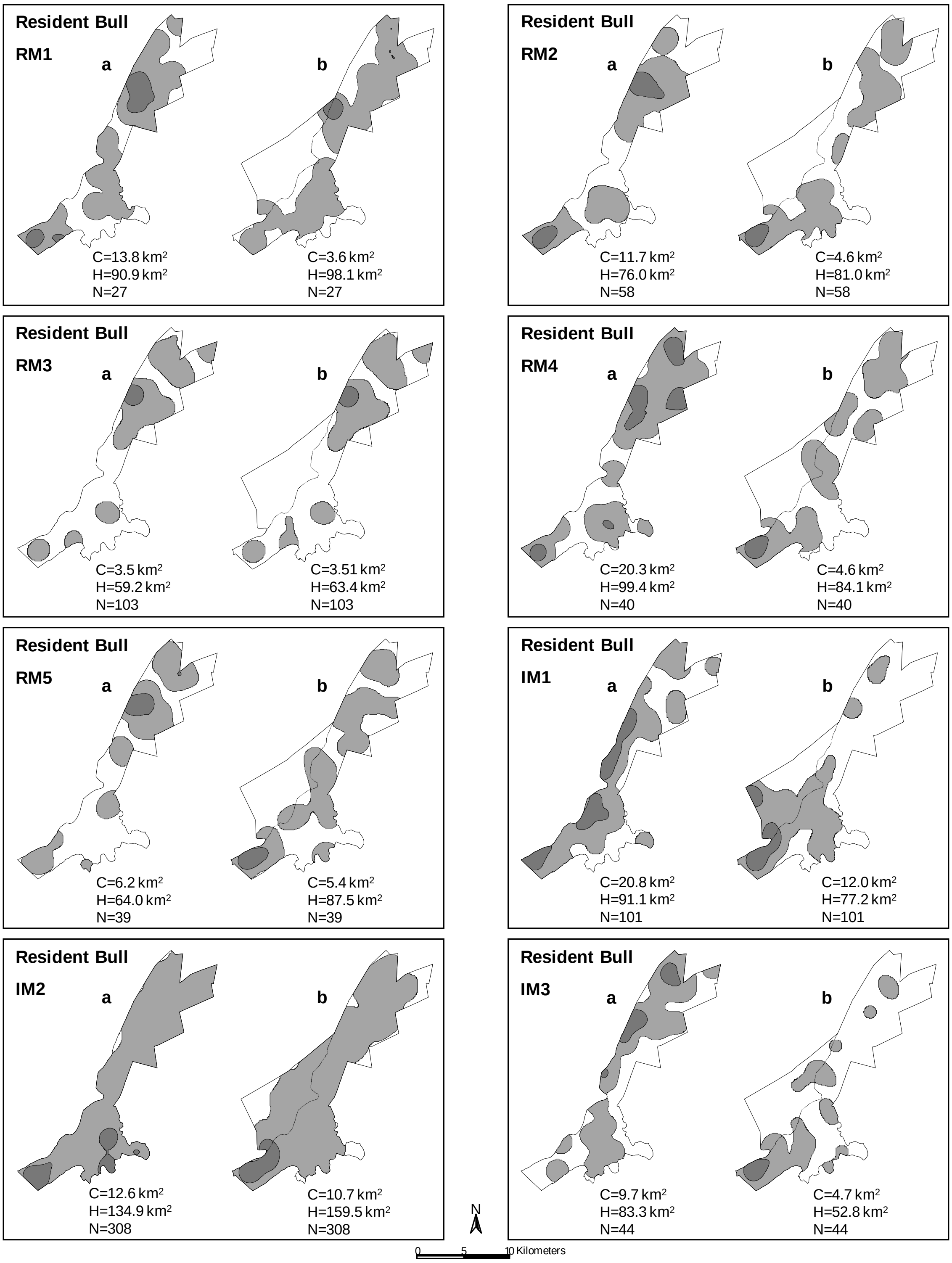

Figure 4. Ranging of the Phinda elephant bulls on Munyawana Conservancy: The effect of the fence removal on the ranging behaviour of the bulls. Two maps are shown for each bull: **(a)** the 13 month period before the fence removal, **(b)** the 13 month period directly after the fence removal. C = Core ranges (50% kernel – dark grey shading) and H = Home ranges (95% kernel – light grey shading). N = number of locations used to calculate ranges for that period.

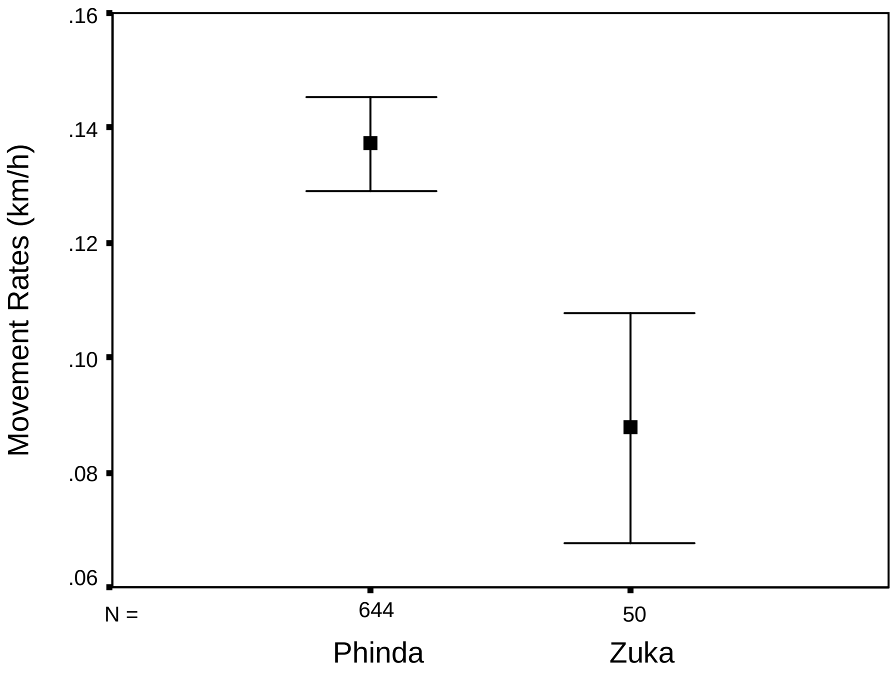

Figure 5. The rate of movement is indicated by points 12 hours apart for subsequent days. (Raw data were used, mean ± 96% confidence limits, N = number of distance data points for each area).

Discussion

Over the last decade, many private reserves and protected areas in South Africa have faced exceptional growth rates in their elephant populations (Mackey et al. 2006) and subsequently reached long-term unsustainable elephant densities (Slotow et al. 2005). This may have an undesirable effect on the habitat to expense of other species and biodiversity (see Kerley et al. 2008). In order to effectively manage elephants in small reserves, it is important to obtain accurate and current information regarding elephant population biology and ecology, and to understand how confinement within a limited area may influence the ecosystem and biodiversity. When small, enclosed areas are enlarged by fence removal between neighbouring properties, it is important to monitor the response of the resident elephant population in order to determine the biological and ecological effect of such a management decision.

During this study, a noticeable difference was observed between the responses of female family groups and bulls to the fence removal and the subsequent increase of the conservation area. The family groups took six months or longer before moving into the new area for the first time, and the majority of these groups only travelled the maximum recorded distance from the old boundary within the new area 11 to 13 months after fence removal. However, the bulls were much quicker to move into the new area and to travel far, with this response being even more rapid amongst the older, recently introduced bulls. These bulls moved independently of time of day, while the family groups preferred moving within the new area during the night. These results may indicate that older mature bulls are more prepared to explore new areas and travel longer distances from known resources, while female family groups may prefer to stay in habitats with known resources. The younger resident bulls were found to react similarly to the family groups. A possible explanation for the introduced bulls more extensive ranging patterns and exploratory behaviour may be simply due to their previous large ranging behaviour in the Sabi-Sands and the fact that these bulls were only introduced into Phinda shortly before fence removal. Previous studies (Stokke and du Toit 2000, 2002) have shown that, sexual segregation does occur, as bulls are far more tolerant to variation in diet quality and can travel longer distances between known resources. The older independent introduced bulls may have used the new area to establish bull areas, which were spatially and temporarily different to the areas used by the rest of the population (e.g. Slotow and van Dyk 2004).

One year after the fence removal, 52% of the Phinda elephant population had still not spent more than 24 continuous hours within the new area. Boone and Hobbs (2004) showed that the effects of fencing are long-lived with some species, and once fences are removed it may take decades to adopt the new area.

A key finding was that the elephants appeared to act cautiously in exploring the new area, as was documented by different measures of spatial and temporal patterns. The cautious behaviour has been validated by numerous studies that have shown that animals adapt their ranging and foraging behaviour to avoid unexplored areas and human-induced disturbance. Poaching activities influence elephant home ranges extensively (Aleper and Moe 2006), while hunting activities cause a movement avoidance effect (Burke et al. 2008). Brown hyaena adapt their foraging behaviour in cattle range areas to forage only around midnight to minimize any chance of encountering potentially hostile humans (Maude 2005), and elephant in Kenya ‘streak’ through corridors mostly at night time, and these areas are excluded from the elephants’ home ranges (Douglas-Hamilton et al. 2005). Several studies (Pretorius 2004, Douglas-Hamilton et al. 2005, Burke et al. 2008) have indicated significantly increased mobility when elephants experience stress, either to human-induced disturbance or when entering unexplored or unsafe areas. This cautious exploration behaviour towards a new unexplored area was observed by the adult bulls entering the new area first for a short distance and short time period before returning to the known area. Furthermore, female groups did not include the new area in their core ranges, visited the new area during the night before returning to the known area during the day time and never spent more than 24 consecutive hours within the new area in the first seven months after fence removal. This cautious behaviour implies that elephant may perceive the new unexplored area initially as threatening. Cautious behaviour declined over time as the animals became more familiar with the new area, spent longer periods in this area, and travelled further into the new area later on.

One may speculate that the elephant’ social, physical and nutritional needs may not have been fully satisfied within the old area, which is why they moved into the new area. Alternately, there may have been sufficient resources within the old habitat with no need for the elephants to rapidly explore the new area. The slow colonisation may indicate that the elephants were not desperate for space and/or resources, and were not restricted by the small reserve size. We speculate that this small reserve size could provide sufficiently from a welfare perspective (see Lötter et al. 2008), in that all social, physical and nutritional needs appear to be met within the existing area. The population had no immediate urge to explore or expand their ranging areas, signifying that there were not strongly stressed, and that from a welfare perspective, elephants can be adequately kept in an area as small as 150 km^2. Note that in such circumstances, over time there may be cumulative negative impacts on the local biodiversity because the elephants may be concentrated in an artificially small area (see Kerley et al. 2008).

This study indicates that the removal of boundary fences to form larger conservation areas (e.g. transfontier parks such as Greater Limpopo Transfrontier Park, Limpopo/Shashe Transfrontier Conservation Area and corridor reserves like Selous-Niassa Wildlife corridor, South Tanzania (Mpanduji et al. 2002); Panyame-Mavuradona Wildlife corridor, Zimbabwe (Osborn and Parker 2003)) may not result in rapid expansion or dispersal of elephants into the new area and an instant reduction of impact on the original area. Therefore, quantification of environmental impact in relation to a gradient of elephant density over time needs to be done (Barratt and Hall-Martin 1991) to ensure a sound understanding of elephant impact.

Although increasing the size of a conservation area could be a popular “hands-off” management approach to deal with increasing elephant populations, it may only be a medium term solution for dealing with high densities of elephants in reserves. Elephants in Kenya responded at large spatial scales and quick temporal scales to corridor linkages between protected areas (Douglas-Hamilton et al. 2005). We found the opposite, the spatial scale of response being relatively small, and the temporal scale of response relatively large. Pachyderms may only gradually expand into new “greener pastures”, but more case studies are required to understand general responses of mega herbivores, like elephants, to fence removal and conservation area expansion.

Consequently, we recommend drawing on the available range of management options to achieve objectives, by increasing land through incorporation and, for example, simultaneously lowering the population size (e.g. culling) and/or growth rate (e.g. contraception) (see Biggs et al. 2008 for overview and appropriateness of options). Another possible management option maybe to create corridor linkages between already existing reserves (Plumptre et al. 2007), if it is not an option to completely join or enlarge the conservation areas with adjacent land. Regular monitoring and research into active management of this species within small and enclosed reserves will provide understanding and potential solutions to reduce impact on biodiversity (see Kerley et al. 2008), or other conflicts with reserve objectives.

CHAPTER 5

HOW IMMUNOCONTRACEPTION CAN CONRTIBUTE TO ELEPHANT MANAGEMENT IN SMALL, ENCLOSED RESERVES: MUNYAWANA POPULATION AS A CASE STUDY.

Abstract

Immunocontraception has been widely used as a management tool to reduce population growth in captive as well as wild populations of various fauna. We model the use of an individual-based rotational immunocontraception plan on a wild elephant, *Loxodonta africana*, population and quantify the social and reproductive advantages of this method of implementation using adaptive management. The use of immunocontraception on an individual, rotational basis stretches the inter-calving interval for each individual female elephant to a management-determined interval, preventing exposing females to unlimited long-term immunocontraception use (which may have as yet undocumented negative effects). Such rotational immunocontraception can effectively lower population growth rates, age the population, and alter the age structure. Furthermore, such structured intervention can simulate natural process such as predation or episodic catastrophic events (e.g. drought) which regulates calf recruitment within an abnormally structured population. A rotational immunocontraception plan is a feasible and useful elephant population management tool, especially in small, enclosed conservation area. Such approaches should be considered for other long-lived, social species in enclosed areas where the long-term consequences of consistent contraception may be unknown.

Key words: adaptive management, immunocontraception, *Loxodonta africana*, population age structure, population growth rate, Phinda Private Game Reserve.

Introduction

Within natural, open conservation systems, large stochastic events such as drought, fire and predation keep populations at a sustainable level by eliminating the old, weak and young (Owen-Smith et al. 2005, Foley et al. 2008, Woolley et al. 2008a, Woolley et al. 2008b). However, within modern conservation areas, especially small, enclosed reserves, natural stochastic events are altered by human management interventions (Woolley et al. 2008a), with more intervention required for smaller reserves (Kettles and Slotow 2009). Within these conservation areas, the occurrences and spread of big fires are often prevented or controlled (but see Woolley et al. 2008b), while natural droughts have limited effects on wildlife populations, as critical resources are usually never a limiting factor due to water and food provision (Gough and Kerley 2006, Druce et al. 2008). The fences prevent natural movement patterns from and into these areas, and predation events are effected and controlled within these areas, as managers determine and restrict the predator-prey ratios, and predator population structure (Kettles and Slotow 2009, Hayward et al. 2009). This can result in eruption of populations which leads to significant environmental problems (Hayward and Zawadzka 2010, Kerley et al. 2008), which then require active management intervention (Mackey et al. 2006, Merrill et al. 2003, Cooper and Herbert 2001, Caughley 1970).

Natural processes should be simulated to achieve management objectives without a negative effect on the system (Walker 1998). However, because active management requires managers to impede the natural processes of nature (Caughley 1976), it can often have unforeseen consequences (e.g. killing of rhino, *Ceratotherium simum*, by elephant, *Loxodonta africana*) (Slotow et al. 2000). This is of special concern for species with complex social systems, e.g. Hamadryas baboons, *Papio hamadryas* (Krebs and Behlert 2006, Rijksen 1981), Lion-tailed Macaques, *Macaca silenus* (Singh and Kaumanns 2005) and elephants (Slotow et al. 2000, Whitehouse and Kerley 2002). Thus, for management interventions to be effective and non-detrimental, a sound understanding of the natural processes is required.

Small, enclosed reserves within South Africa are experiencing eruptive elephant population growth, which is an increasing concern to conservation biologists, ecologists and wildlife managers (Garai et al. 2004, Slotow et al. 2005, Kerley et al. 2008). In the older, larger populations, these elephants were introduced as orphans from culls in Kruger National Park (Slotow et al. 2005). These introductions have resulted in very young, fast-growing populations, with no or very low, adult senescence (Mackey et al. 2006, Slotow et al. 2005). The pressure exerted by increasing density of animals can cause environmental damage (Hayward and

Zawadzka 2010) and changes in biodiversity (Cumming et al. 1997, Lombard et al. 2001, Wiseman et al. 2004). Therefore, overabundance and rapid growth rates may require active management (Biggs et al. 2008, Owen-Smith et al. 2006).

There are two natural processes that could control elephant population numbers. One process is natural mortality, particularly of young animals (see Woolley et al. 2008a, Woolley et al. 2008b). During episodic catastrophic events (e.g., drought), entire cohorts of juvenile elephants can be lost (Foley et al. 2008, Woolley et al. 2008a). The second process is the regulation of female inter-calving intervals (and, less importantly, age of maturation - see Mackey et al. 2006) by environmental conditions (Trinkel et al. 2010); under adverse conditions, inter-calving intervals should increase (Wittemyer et al. 2007).

Immunocontraception has been used as a management tool around the world for numerous years to restrict rapid population growth in captive as well as wild populations of many animal species i.e. feral horses (*Equus caballus*) (Kirkpatrick et al. 1992, Powell and Monfort 2001, Turner and Kirkpatrick 2002); Prezewalski's horses (*Equus prezwalskii*) and banteng (*Bos javanicus*) (Kirkpatrick et al. 1995); white-tailed deer (*Odocoileus virginianus*) (Mcshea et al. 1997, Naugle et al. 2002); Brandt's vole (*Microtus brandti*) (Shi et al. 2002); Tule elk (Cervus *elaphus nanodes*) (Shideler 2000); and African elephants (Whyte and Grobler 1998, Fayrer-Hosken et al. 1999, Delsink et al. 2006). Immunocontraception of African elephants has proven safe (Delsink et al. 2006, Bertschinger et al. 2005) and effective in reducing population growth rates (Delsink et al. 2006, Fayrer-Hosken et al. 2001, Kirkpatrick 2005, Delsink et al. 2005). Consequently, immunocontraception can be used to prevent female elephants from conceiving, or to increase the span of calving intervals of each individual female, and thereby reduce population growth. However, immunocontraception can reduce the existing population size only when it decreases the birth rate to a level that is below the mortality rate. This reduction in birth rate will subsequently age a population over the long term (Bertschinger et al. 2008), assuming that age-specific mortality rates are constant. By preventing calving or by prolonging calving intervals, immunocontraception can be used to simulate calf mortalities from predation or prolonged bouts of adverse environmental conditions (e.g. droughts).

Immunocontraception has a minimal influence on elephant social behaviour in the medium term (Delsink et al. 2006, Bertschinger et al. 2005, Kirkpatrick 2005). However, it has been suggested that social problems may occur in elephant populations treated with prolonged use of immunocontraception that is intended to prevent any calves being born into a population (Poole

1993, Kerley and Shrader 2007). Potential social problems include the lack of allomothering experience within family groups, due to prolonged absence of newborn calves, and depression amongst adult females arising from their continual oestrus cycling as an inability to conceive and give birth (Kerley and Shrader 2007). To overcome these potential long-term effects, females can be allowed to give birth periodically. The effects of such births on populations, and how to manage such reversal of contraception at a population level, is unknown. The rotational use of contraception can simulate natural processes within a small, enclosed population, but it remains important to monitor and study the social and behavioural effects.

This study attempted to reveal some knowledge and understanding on the rotational contraception on a species at the population level. The feasibility of implementing individual-based contraception of elephants has been demonstrated elsewhere (Delsink et al. 2007). Here we used the Munyawana elephant population as a case study to demonstrate an example of individually-based, rotational immunocontraception used to simulate the effects of natural mortality which increase inter-calving intervals. We use population models to determine potential effects of immunocontraception-based management plans on elephant population size and age structure.

Study area

This study was conducted within the Munyawana Conservancy, KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E). Initially, Phinda Private Game Reserve (Phinda) was established in 1991, with an area of approximately 150 km^2. During August 2004, the boundary fences between Phinda and two neighbouring reserves, Zuka and Mziki Pumalanga were removed, forming the Munyawana Conservancy (185 km^2) (see Fig. 1). During May 2006, the boundary fences were removed between Munyawana Conservancy and the neighbouring reserve, Sutton, increasing the area of the conservancy to 207 km^2 (see Druce et al. 2008).

The vegetation types within the Munyawana Conservancy were Sand Forest (Low and Rebelo 1996; Type 3), Sweet Lowveld Bushveld (Low and Rebelo 1996; Type 20), Natal Lowveld Bushveld (Low and Rebelo 1996; Type 26), Lebombo Arid Mountain Bushveld (Low and Rebelo 1996; Type 13) and Coastal Bushveld-Grassland (Low and Rebelo 1996; Type 23). One perennial river, the Mzinene River, flows from west to east through the southern section of the conservancy, and dams were extensively distributed throughout the properties. During the rainy season, surface water was extensive; while some of these dams retain water all year round, other dams were supplied with borehole water during the dry periods, i.e. water was always available.

The Munyawana Conservancy has a summer rainfall regime and temperatures range from an annual mean minimum of 10 °C to an annual mean maximum of 35 °C.

Methods

Munyawana Immunocontraception Management Plan

The Munyawana management team was greatly concerned about the continuous elephant population growth within the small and enclosed system. By the end of 1994, a total of 58 elephants had been introduced into Phinda from Gonarezhoa in Zimbabwe and from former Kruger culling operations (Slotow et al. 2004). Within 10 years, the Phinda elephant population almost doubled in numbers, with the average annual population growth rate since introduction equalling 9.4%. The elephant population was monitored on a daily basis from March 2003 through to July 2006 (end of data used in this study, but monitoring is still continuing in 2009). As many elephant as possible were located each day, and general location data, identities of adult individuals present and behavioural activities (in general, as well as musth, oestrus behaviours and newborn calves) were recorded. All population demographic data until July 2006 were used in the models. Monitoring of the populations within the inclusive reserve began once these areas became part of the conservancy. All individual elephants were known, as well as the family groupings.

During July 2003 the population was reduced from an estimated 107 individuals to 66 individuals through the translocation of four family groups to other private game reserves in South Africa. In July 2006, the total elephant population within the Munyawana Conservancy consisted of 98 individuals, with 20 independent bulls and seven family groups. Of this, the Phinda population comprised 88 individuals, with 19 independent bulls and five family groups. The Zuka population consisted of three young individuals and the Sutton elephant population comprised one family unit made up of seven individuals. Neither the Zuka nor the Sutton populations amalgamated into the Phinda population during this study period, and the Sutton group has subsequently (during November 2007) been translocated from the reserve.

The 2003 translocations reduced the breeding population to a more manageable size (21 sexually mature females) and during May 2004 an immunocontraception plan (ICP) was implemented. The aim of this ICP was to reduce the overall population growth rate, but not to completely prevent conception within the entire female population. The proposed ICP allowed young mothers to have their first calf before being included in the ICP. It also allowed females to calve on a rotational basis within each family group. Through this, the ICP aimed to increase the inter-calving interval of individual females within each family group, but to still allow the social needs of the family groups to be met, in that calves would still be born into the groups on a continuous and regular basis. Births would also be rotated between the females within each family group. The ICP allowed one young calf to be born into each family group at least every two to three years. A further aim of this ICP was to create a more natural population structure, with newborn births evenly spread over time. Herds derived from orphan populations tend to be synchronised in their calving as the introduced female orphans all tend to reach sexual maturity at the same time and, therefore, give birth to their calves at similar times (Slotow et al. 2005, H.C. Druce, pers. obs.). During the elephant immunocontraception darting operations, the contraceptive was administrated by methods described in (Delsink et al. 2007). All the immunocontraception darting procedures during 2004 – 2007 were done from ground, either from vehicle or on foot. Annually the same marksman administered the contraceptive remotely by means of drop-out darts fired from a Dan-Inject dart gun and thereafter darts were retrieved to ensure appropriate treatment.

Immunocontraception Model

An individual-based rotational spreadsheet model was developed to make projections of the size, growth rate and age structure of the Munyawana elephant population under a set of potential management immunocontraception intervention plans. More specifically, we examined the effect of altered inter-calving intervals and preventing females from conceiving their first calf upon sexual maturity. To determine the robustness of our projections, we tested the sensitivity of the model projections to realistic variations in the demographic parameters (age at sexual maturity, time to conceive after release from contraception, natural calving interval).

The demographic parameters incorporated in this model were: (1) age of sexual maturity of females (age of first oestrus, with assumption of first conception), (2) calving interval (average interval between consecutive births for a mother), (3) birth sex ratio, (4) maximum age of individuals, and (5) age at menopause (see Mackey et al. 2006) for parameter details and calculated methods). Additional management parameters modelled were: (5) contraception implementation age (allowing or preventing females from conceiving their first calf upon the age of sexual maturity), and (6) conception time (the time for a cow to conceive upon being released from contraception).

The parameter values were constant for the birth sex ratio, which was 1:1 (Mackey et al. 2006, Laws et al. 1975, Moss 2001), maximum age of individuals [60 years (Mackey et al. 2006, Whyte et al. 1998)] and the age of menopause [50 years (Moss 2001, Owen-Smith 1988)]. Female elephants may reach sexual maturity as late as 17 years (Laws et al. 1975), and will typically produce the first calf two years later (Owen-Smith 1988, Sikes 1971, Poole 1994). However, Mackey et al. (2006, 2009) calculated the average age of female sexual maturity in four small, enclosed reserves to be between 8 and 10 years. The average age of sexual maturity of the Munyawana population was previously thought to be 10 years (Mackey et al. 2006), but additional data up to 2009 indicate this to be nine years. The inter-calving interval of cows is between four and five years (Owen-Smith 1988, Moss 1988, Moss 2000), with estimates as high as four to nine years (Estes 1991). However, recent studies in enclosed populations in South Africa determined calving intervals at between three and four years (Mackey et al. 2006, Mackey et al. 2009). Again, newer census data up to 2009 (but before immunocontraception took effect) for Munyawana indicate average calving interval has reduced from four years (Mackey et al. 2006) to three years.

Moss (1988) observed that female elephants experience very short oestrus cycles of on average four days with females coming into oestrus throughout the year. Sufficient field testing has not yet been done, but estimates of the time for an elephant cow to conceive upon being released from contraception vary from 12 months (Fayrer-Hosken et al. 2001), 12 to 18 months (D. Grobler, CatchCo Africa, pers. comm.), or may be approximately equal to the number of years an elephant cow has been subjected to vaccination (Bertschinger et al. 2008).

The different contraception scenarios were simulated by adjusting a single parameter per scenario and keeping the rest of the parameters at the baseline value (Table 1). We assumed contraception was 100% effective in preventing conception in treated females (Delsink et al. 2006, Bertschinger et al. 2005). Model simulations were done for 20 years (2006 to 2026) to obtain population projections on a timescale which is of relevance to management decision making (Fig. 2). Density dependent regulation was excluded from this simulation model because of the time-scales of the model, time-lags associated with the long generation times and 22-month gestation periods, and the young age structure of the population make changes in natural rates of senescence unlikely (As a young orphan introduced population, none of the adult elephants exceed the age of 60 within the 20 year modelled time frame). Similarly, no stochastic mortalities (drought, fire and predation) were included in the model, as the model was specifically aimed at the known Munyawana population and because, due to intensive macro-management within the small, enclosed environment, stochastic events are unlikely to impact the elephant population [artificial water sources are provided (Druce et al. 2006), fire is managed (pers. Obs.), and lion groups size kept small resulting in no lion predation of elephant (Hunter et al. 2007)]. The purpose of the model is to show the ability to manipulate the population, through selective interventions, to make it more natural in structure. Therefore to use individual-based rotational immunocontraception as an adaptive management tool to simulate natural mortality of young, along with natural environmental effects on female reproduction by ensuring some prolonged inter-calving intervals.

The age structure of the population was determined by assigning each individual into one of five age classes (infant, juvenile, intermediate, sub-adult and adult). The adult age class was further sub-divided into smaller age categories (see breakdown in legends of Fig. 3 and Fig. 4). The absolute numbers of individuals per each age class were calculated at the end of the final year of the simulation (i.e. 2026). The age structure was calculated for the entire population as well as each family group/herd.

Results

Changes in projected population size and growth rate were described for a 20-year span (2006-2026) of the actual contraception plan (as decided by the Munyawana management team separately for the three populations –Phinda, Zuka and Sutton), other contraception scenarios and no-contraception application. The projected effects of contraception on elephant population size showed that there was a large difference in population size over a 20-year period between a non-treated population and a treated population (Table 1, Fig. 2). Annual growth rates for the 20-year period for a non–treated population was 7.58% versus 4.2% for the Munyawana immunocontraception plan that is currently being implemented (Table 1). The slowest overall growth rate was 3.19% for the Munyawana population (Scenario 6) in which females were prevented from conceiving their first calf until 8 years after achieving sexual maturity – producing the first calf at 19 years. The highest projected value (5.06% annual growth rate) for any scenario with contraception was Scenario 7, which had a 6-year calving interval (Fig. 2).

Under the current immunocontraception plan, the Munyawana population would double after 18 years, while the same population would double within 10 years without any contraception implementation (Table 1). When the calving interval was lengthened to longer than 6 years and prevention of the first calf (such as Scenario 6 and 8) was implemented, the population doubling time was projected to be 20 years or longer.

The Zuka population, which is not under a contraception program, had the greatest overall growth rate of 8.73 %. If the Zuka population continues to be left out of the contraception plan, it will double in only 6 years.

Sensitivity analyses indicate the response of the projected elephant population growth rates to changes in the demographic parameters of the model, or the robustness of model projections to change in demographic parameters. Population projections were most sensitive to changes in calving interval and the implementation age of contraception (i.e. whether a female's first calf was delayed). Changes in calving interval produced relatively large changes in population growth rate, with an increase from six to ten years resulting in a reduction of 1.58% in annual growth rate (calculated over 20 years) from 5.06% to 3.48%. Changes in implementation age of contraception from ten to eight years (i.e. if sexual maturity is at nine years of age, therefore by delaying the first born calves), produced a reduction of 0.95% in annual growth rate. The model projections were not particularly sensitive to age of sexual maturity and the length of conception time after release from contraception. Changes in age of sexual maturity produced relatively small changes in population growth rate, with an increase from eight to ten years resulting in a reduction of 0.33% in annual growth rate (from 4.36% to 4.03%). Increasing the conception time from one to three years resulted in a reduction of only 0.03% in annual growth rate (from 4.16% to 4.13%).

The model was used to project the probable changes to the age structure of the population under various contraception scenarios (Fig. 3). The initial population age structure before any immunocontraception had taken affect during 2006 was used as the baseline data (Fig. 3a) to simulate different future outcomes, where after comparisons of age structure were made between no-contraception, 100% and a rotational contraception from predicted model results at year 20 (i.e. 2026). When no-contraception was applied to the Munyawana population, the model projections indicated that the bulk of the population comprised young animals, and as the breeding population increased in size over time the recruitment of young also increased (Fig. 3b). When a continual 100% contraception rate was applied, there were no new calves added to the population and the average age of individuals in the population has increased; this ultimately had the effect of aging the population (Fig. 3c). With rotational immunocontraception application, the Munyawana population produced a limited number of calves, subsequently resulting in a more even age structure (Fig. 3d). The population age structures for 100% immunocontraception were very different from those projected for rotational contraception scenarios.

The total number of adult females (females older than 13 years of age) at the end of 2026 for the 100% contraception rate was 41 (Fig. 3c), with 77 adult females for the no-contraception application (Fig. 3b) and a total of 51 adult females for the rotational contraception application scenario (Fig. 3d). The number of adult females present within the population indicates the reproductive potential and future growth rate.

Similar projected effects were found on the age structure of individual family groups/herds and that of the overall Munyawana population under the various contraception scenarios (Fig. 4a, 4b, 4c). At the end of the 20-year modelled period under rotational contraception, the average age of individuals in the family group had increased and their growth rates had been reduced, but they still contained calves that had been born into each group over the period (Fig. 4c). A large number of independent males were contained in family group 3 as a result of a male-biased calving documented in this family group during 2006, whereas family groups 4 revealed a female calf-biased during 2006 which results in a larger amount of reproductive females at the end of the 20-year modelled period.

Table 1. Modelled elephant population growth rate, population doubling time and population size for the contraception period 2006-2026.

Modelled scenarios for Munyawana elephant population	**Parameters**				**Annual growth rate (%)[v]**	**Population doubling time (years)[vi]**	**Projected population size**	
	Age of sexual maturity (years)[i]	**Implementation age (years)[ii]**	**Conception duration (years)[iii]**	**Calving interval (years)[iv]**			**2006 (start)**	**2026 (end)**
Munyawana- current contraception plan	The combined Phinda & Sutton treated, Zuka non-treated plans				4.20	18	98	230
Munyawana- no-contraception plan	9	-	-	3	7.58	10	102[vii]	469
Scenario 1	9	10	1	8	4.16	18	98	217
Scenario 2	9	10	3	8	4.13	18	98	216
Scenario 3	8	9	2	8	4.36	17	98	228
Scenario 4	9	10	2	8	4.15	18	98	216
Scenario 5	10	11	2	8	4.03	19	98	211
Scenario 6	9	8	2	8	3.19	>20	98	178
Scenario 7	9	10	2	6	5.06	15	98	259
Scenario 8	9	10	2	10	3.48	20	98	196
Current contraception plan for the individual elephant populations within the Munyawana Conservancy								
Phinda	9	11	3	8	3.71	19	87	184
Zuka-no-contraception	9	-	-	3	8.73	6	4	25
Sutton	8	10	3	9	5.26	12	7	21

[i] Parameters for the age of sexual maturity were 8 years, 9 years (baseline) and 10 years.
[ii] Parameters for the contraception implementation age were 8 years (prevent the first calf and only allow the first calf at 19 years after allowing an 8 year calving interval) or 10 years (baseline – allows the first natural birth, if the cow conceive at the baseline of 9 years age at sexual maturity).
[iii] The length of time that a female was released from contraception to ensure conception, with the parameters of 1 year, 2 years (baseline) and 3 years.
[iv]Parameters for the contraception induced calving intervals were 6 years, 8 years (baseline) and 10 years.
[v] The growth rate was calculated for the 20-year time span (2006-2026) from the slope of regression on the natural log of population size against year.
[vi] The time it takes for the population to double the starting numbers.
[vii] The Munyawana elephant population total at the beginning of 2006, was calculated as if no females were on contraception for the past 3 years and would have conceived, accordingly a calving interval of 3 years was maintained from the age of the youngest calf

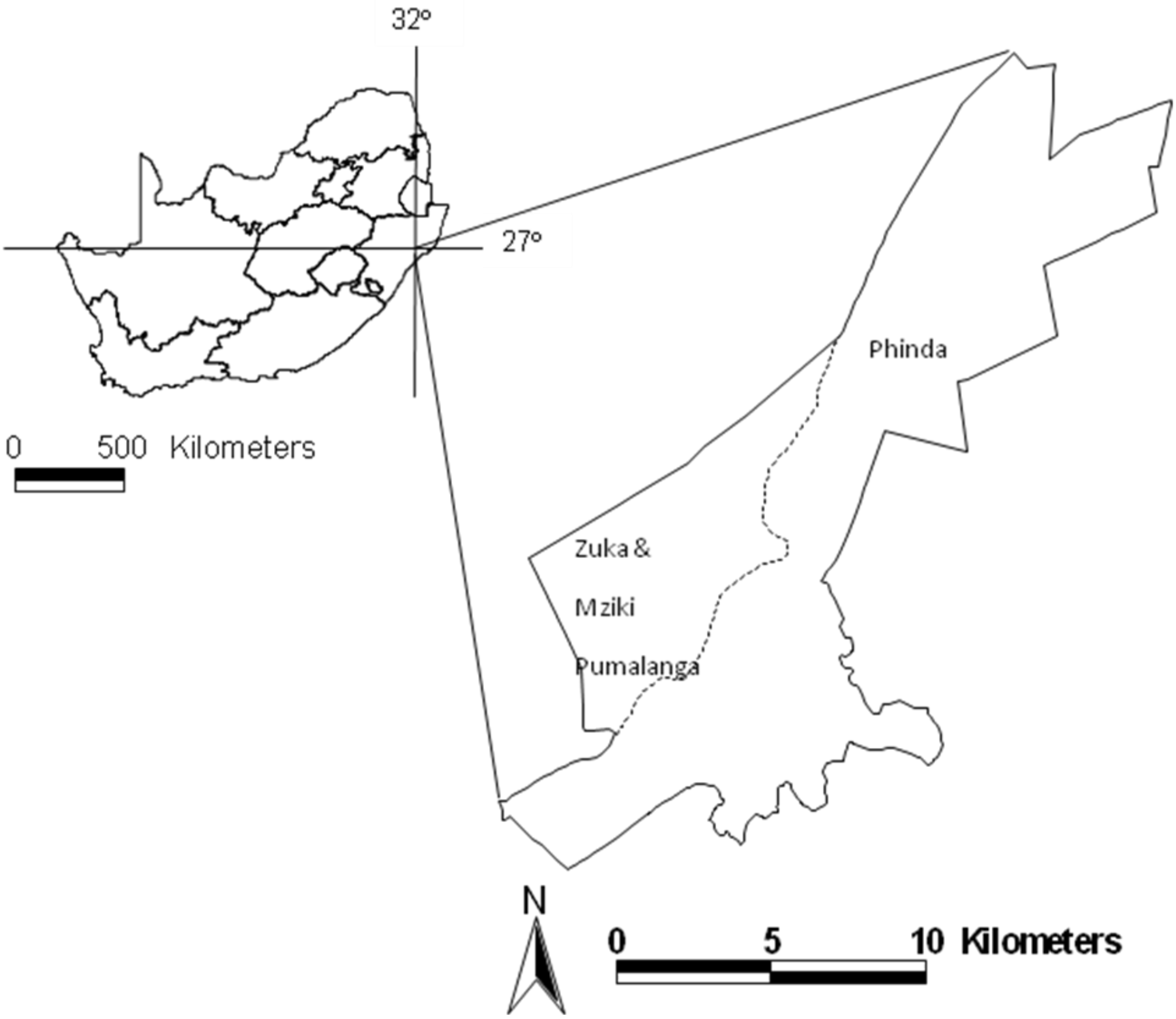

Figure 1. Munyawana Conservancy. The dashed line indicates the position of the boundary fence between Phinda and the new sections of Zuka, and Mziki Pumalanga before the fences were removed during August 2004.

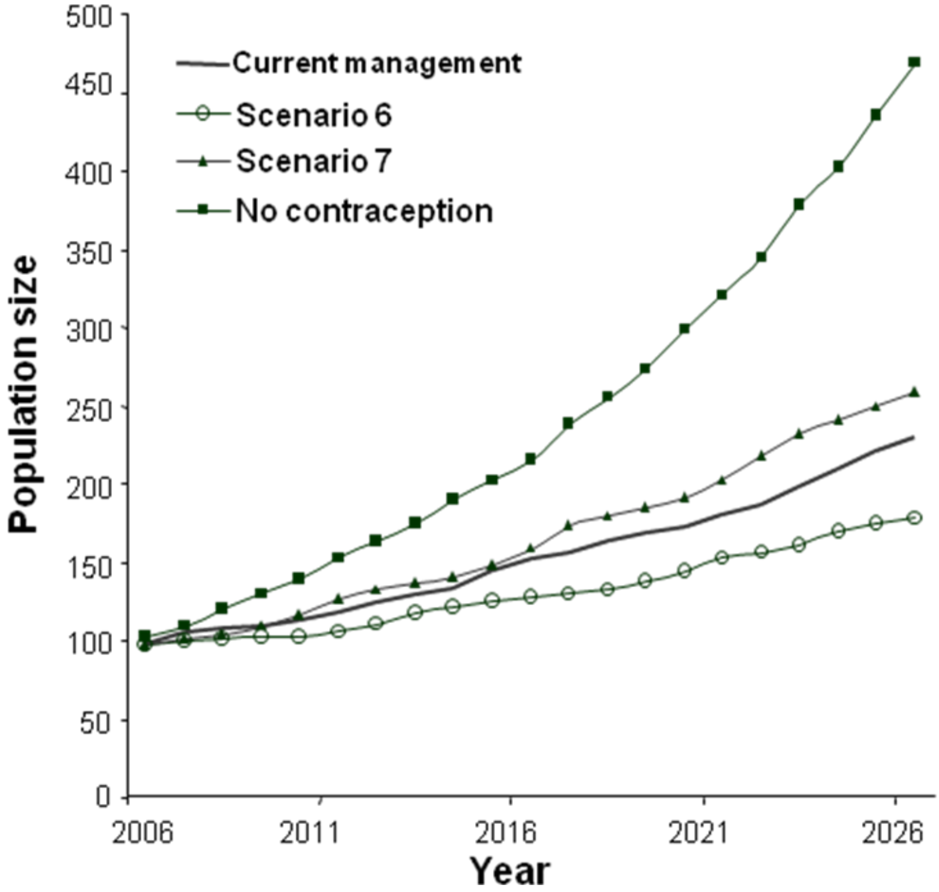

Figure 2. Projected population size for the Munyawana elephant population under different immunocontraception scenarios for a 20-year time period. Results are shown for the current Munyawana immunocontraception plan, no application of immunocontraception on the population, and two contraception scenarios (Scenarios 6 and 7) that resulted in the most extreme projections. Scenario 6 was the prevention of the first calf and allowing the female to calf at 19 years of age, with a baseline contraception-induced calving interval of 8 years thereafter. Scenario 7 examined a shortened calving interval of 6 years.

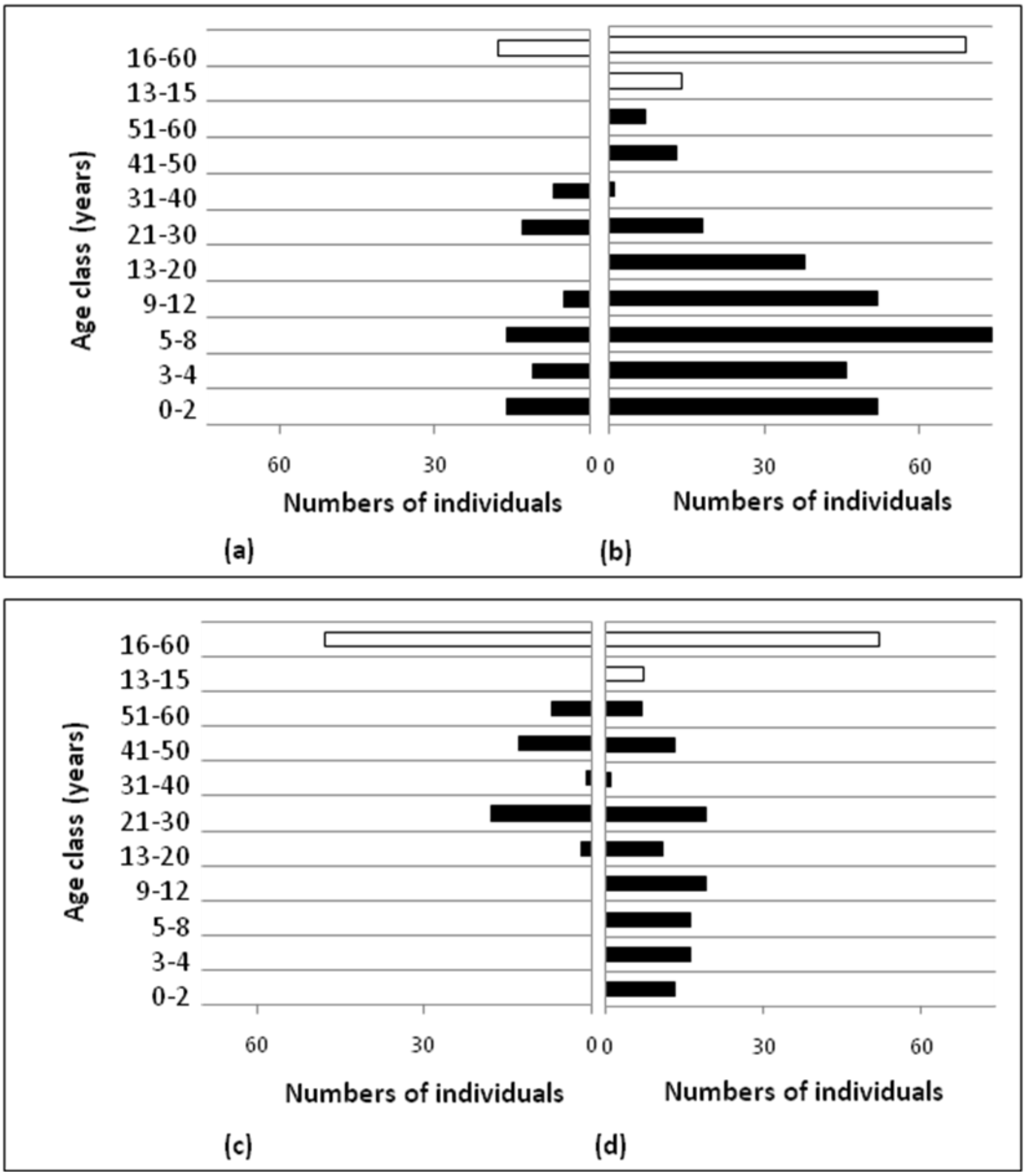

Figure 3. The projected Phinda elephant population divided into age classes represented as absolute numbers under different immunocontraception scenarios. The age classes are classified as 0-2 years: infant, 2-4 years: juvenile, 5-8 years: intermediate, 9-12 years: sub-adults, older than 13 years are classified as an adult. Adult bulls are presented by white bars (with only two age classes), while all the individuals in the breeding herds are represented by the black bars which include males <13 years.
(a). The Phinda elephant population in 2006 before any effects of immunocontraception had taken affect.
The projected Phinda elephant population in 2026,
(b). without any application of immunocontraception
(c). with a 100% application of immunocontraception
(d). with a rotational application of immunocontraception, as the current Phinda implemented immunocontraception plan.

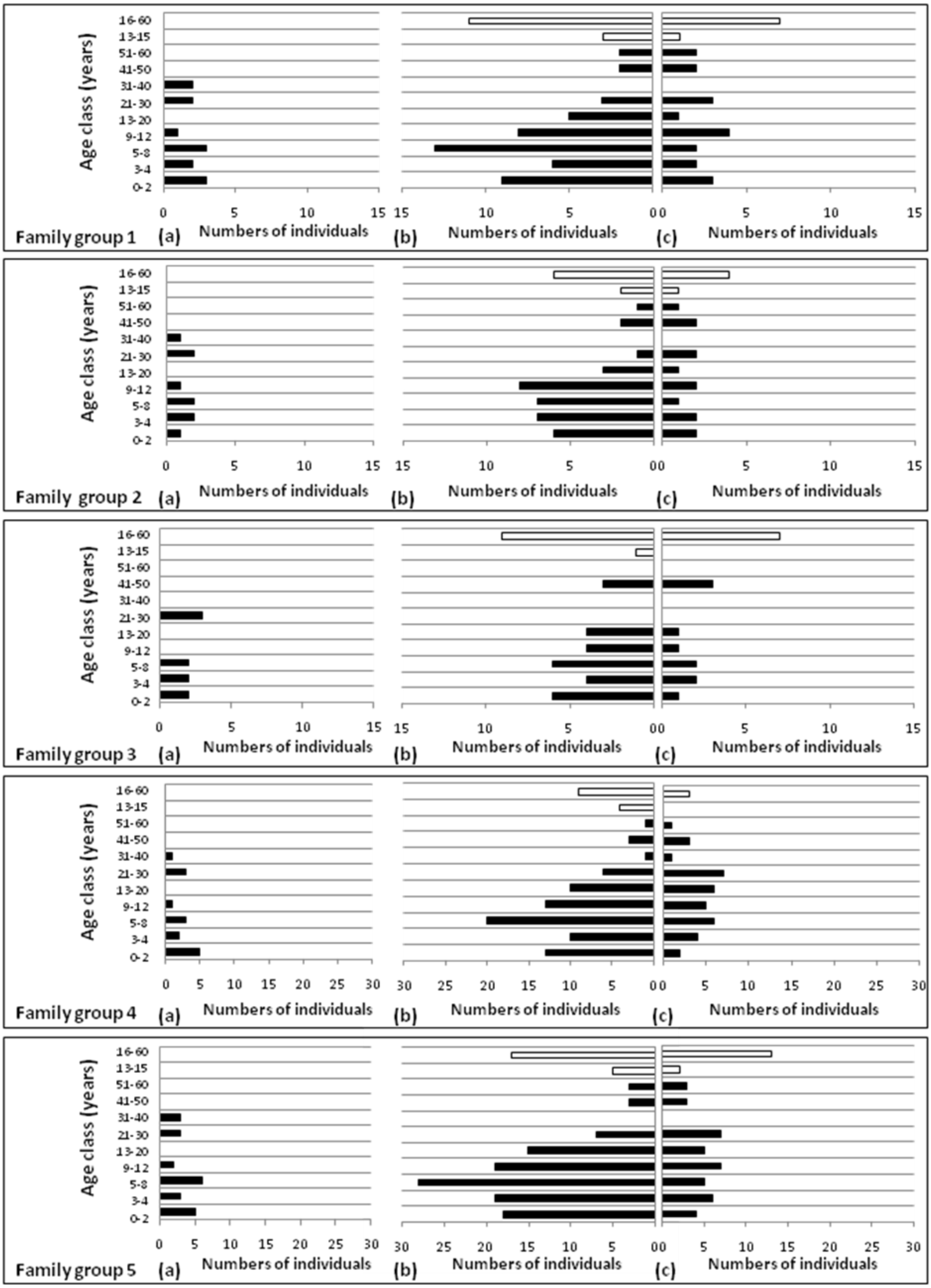

Figure 4. The projected Phinda elephant population as family groups and divided into age classes represented as absolute numbers under different immunocontraception scenarios. The age classes are classified as 0-2 years: infant, 2-4 years: juvenile, 5-8 years: intermediate, 9-12 years: sub-adults, older than 13 years are classified as an adult. Independent adult bulls born into family groups are presented by white bars (with only two age classes), while all the individuals in the family groups are represented by the black bars which include males <13 years.
(a). The Phinda elephant population in 2006 before any effects of immunocontraception had taken affect.
The projected Phinda elephant population in 2026,
(b). without any application of immunocontraception
(c). with a rotational application of immunocontraception, as the current Phinda implemented immunocontraception plan

Discussion

Immunocontraception is a tool that can be adapted to meet different management objectives in reducing population growth (Delsink et al. 2006, Delsink et al. 2007, Stout and Colenbrander 2005). This study showed that a rotational approach to an immunocontraception plan can be a useful tool to age a population and thereby stabilise its age structure; yield a reduced population growth and prevent irruption of young populations; allow for management of populations, family groups and individuals in relatively small reserves enclosed by fences.

The current Munyawana immunocontraception management plan approximately halved the population growth rate and doubled the population's doubling time, compared to when no-contraception was implemented. The results also provide some insight into which demographic parameters may be most important for determining rate of population growth. Mackey et al. (2006) also concluded that calving interval was more important for regulating elephant population growth than any other parameters we evaluated.

The sensitivity analyses indicated little change in population growth from variation in the other parameters, showing that the model is fairly robust. The magnitude of natural variation in demographic parameters should have little effect on model projections. Due to this projected relative insensitivity of elephant population growth to variation in demographic parameters, extremely complex immunocontraception plans may not necessarily be required. What will have the greatest effect on population growth is whether the population is treated or not; potential natural variation in demographic parameters in the short- and medium-term will lead to only minor effects on population growth. However, the population age and sex structure, as a demographic parameters are important to determine future reproductive potential, especially if management ceases future contraception treatment. The age structure will be affected by the natural old age senescence within a population and the proportion of births will be directly related to the proportion of adult females in the population at the time.

With a rotational immunocontraception plan, the population should undergo a stabilisation of the age structure. This should result when annual recruitment is reduced to the same level as senescence (the only significant source of elephant mortality in South Africa's small enclosed reserves, but see Woolley et al. 2008b). Alternatively, for a more extreme effect, a contraception rate of 100% over a long term would result in no calves being added to the population with the consequence that the population would age, due to the average age of individuals in the population increasing over time. If this rate were applied over a longer time period, it would result in a decrease in the population through senescence without births, a possible alternative to culling.

The long-term effects of immunocontraception of female reproductive health are still uncertain. Delsink et al. (2005) showed that ovulation and oestrus cycles remained the same after five years of continuous immunocontraception of female elephants. Immunocontraception is said to be reversible by some researchers (Bertschinger et al. 2005, Fayrer-Hosken et al. 2001, Kirkpatrick 2005), but some studies have shown that the continuous long-term use of the immunocontraception vaccine porcine zona pellucida (PZP) may cause ovarian disfunctioning (Kirkpatrick et al. 1995), a slow return of fertility (Turner et al. 2007) or even the permanent loss of fertility (Kirkpatrick et al. 1995). The possibility that the long-term use of PZP might cause infertility in elephant females still needs to be tested (Poole 1993, Stout and Colenbrander 2005).

However, many of the social and behavioural concerns previously raised about prolonged, continuous and indefinite use of immunocontraception in elephants may be reduced, or eliminated, by the use of a rotational, individual-based contraception program. Concerns have been raised about the negative effects on group behaviour that could arise from immunocontraception plans that completely prevent offspring being born into a herd (Fayrer-Hosken et al. 1999, Perdok et al. 2007). Additional negative effects may include changes in feeding patterns and spatial use (Kerley and Shrader 2007), the lack of allomothering (as described by Lee 1987) affecting the learning of first-time mothers (Kerley and Shrader 2007), and depression in mature females resulting from their inability to calve for a long period of time (Kerley and Shrader 2007). Because a rotational, individual based immunocontraception plan would permit all females to calve, but with prolonged inter-calving intervals, these potential negative effects of contraception should be reduced. Thus, immunocontraception following such a plan should not pose significant social or behavioural concerns and/or threats.

Managers of large reserves with a high elephant population density may question the realistic effect of immunocontraception as a management tool. Delsink et al. (2006) suggested a 'mass-darting approach' for large populations, which is a more flexible approach than the individual-based approach. When a large population of elephants is known on a herd/family group level, the rotational mass darting approach could be applied to family groups/herds within a population, whereby contraception darting can be rotated between herds at a management determined time period. Further modelling and future work on testing mass application methods will need to be undertaken.

Stochastic events naturally control the population growth rate, size and age structure, while eliminating the population's old, sickly, weak and young (Owen-Smith et al. 2005, Foley et al. 2008, Woolley et al. 2008a). Where management either controls or prevents the occurrence of normal natural stochastic events, eruptive populations arise, especially within small, enclosed conservation areas (Mackey et al. 2006). The simulation of natural events (like drought and predation) by management will have consequences on the population demographics and behaviour, which might result in problem behavioural responses as seen in elephants (Slotow et al. 2000, Bradshaw et al. 2005, Gobush et al. 2008), predators (Balme et al. 2009) and primates (Krebs and Behlert 2006, Rijksen 1981). Therefore management requires a sound understanding of the natural processes, social demographics and behavioural requirements applied to the specific species involved. Hereafter with this understanding and essential monitoring, simulation of natural processes can be used in adaptive management plans.

Management Implications

Immunocontraception can be used as a tool to simulate natural stochastic events like drought, however a continual drought with complete calf mortality (e.g. by implementing a 100% contraception continually) is not natural. Therefore rotational immunocontraception can be used to simulate drought cycles, whereby four years of drought are simulated and thereafter four years of non-drought, which would allow cohorts of births to occur. Another approach can be to simulate predation events by using an individual-rotational immunocontraception application approach, whereby selected females are treated and prevented from conceiving, as to simulate that those calves are removed from the population. Therefore rotational, individual-based immunocontraception can be a useful, practical, effective and flexible management tool to include as part of an adaptive elephant management plan.

Ethical Approval

Ethical approval for the use of the vaccine was obtained from University of Pretoria's Animal Care and Use Committee, Project number: 36-5-251 (Project name *Non-lethal control of African elephant (Loxodonta africana): Game reserves and respective elephant populations*). The South African Medicines Control Council issued permits and approval for the "Use of an unregistered medicine in terms of Section 21 of Act 101 of 1965". (Permit numbers SP/35/2002, SP/11/2003, SP/51/2004 and SP/166/2004) (Delsink 2006). During the elephant immunocontraception darting operations, the contraceptive was administrated by approved methods, as described in (Delsink et al. 2007, Berthschinger et al. 2008).

CHAPTER 6
THE INTERMEDIATE-TERM EFFECTS OF PZP IMMUNOCONTRACEPTION: BEHAVIOURAL MONITORING OF THE TREATED ELEPHANT FEMALES AND ASSOCIATED FAMILY GROUPS.

Abstract

Rapidly increasing elephant populations are raising concerns, especially within enclosed conservation areas in southern Africa. Elephant immunocontraception is an effective management tool, enabling conservation managers to control elephant population growth rates, but the behavioural consequences of this intervention needs to be studied more intensively and over longer periods of time. This is especially important as the potential risk of disturbance, and the ethical concerns over welfare of wildlife, can compromise the success of management interventions. We determined the influence of immunocontraception application on behaviour of family groups. The disruption effect of immunocontraception darting on the family groups within the population was minimal, with no significant changes found in the mobility of family groups. Analysis of family group fission and fusion indicated that family groups spent more time alone during the second year of contraception application; this could be a consequence of maturation of the relatively young population. There was no significant relationship between bulls' association with family groups and the number of oestrous females present in the group. With negligible short-term effects on the behaviour of family groups, immunocontraception may be an effective, flexible management tool. Furthermore, this study showed that monitoring and assessment of behavioural assays during active adaptive management is important to determine conservation out-comes and to ensure future management success.

Key words: *Loxodonta africana*, porcine zona pellucida (PZP), behavioural monitoring, grouping tendency, bull association.

Introduction

The immense increase in human population over the past century throughout Southern Africa has diminished the land available to wildlife, especially for the Africa elephant (*Loxodonta africana*), to a fraction of their former range (see Chadwick 1992). Wildlife now competes for land with humans. In South Africa, wildlife species that cannot easily co-exist with humans are restricted to conservation areas, as there is no longer space available outside of these areas. Consequently these protected areas have become 'safe havens' for wildlife (Kettles and Slotow 2009, Lotter et al. 2008). Due to the dramatic decrease in availability of land, the restriction that fencing perimeters pose to protected areas by preventing seasonal migration and ever-increasing population sizes, enclosed populations need to be actively managed (Owen-Smith et al. 2006). Humans have already massively interfered with nature by restricting natural processes and must take responsibility for this interference (Lotter et al. 2008). Managers of protected areas aim to minimise disruption on the natural behaviour of animals during management interventions (Sonnekus and Breytenbach 2001). Consequently, it is important to determine the effect of wildlife management interventions to ensure they are in the best interests of the species involved. The potential risk of disturbance to a wildlife population can compromise the success of management interventions (Kettles & Slotow 2009, Slotow and Hunter 2009). Therefore continual monitoring and standardised assessment of behavioural changes and abnormalities which may occur during active adaptive management is vitally important to determine conservation outcomes and to ensure future management success (Biggs et al. 2008).

Over the last three decades, an immunocontraception vaccine derived from porcine zona pellucida (PZP) has been developed, applied and shown to be effective in controlling reproduction in a variety of captive zoo species (Kirkpatrick et al. 1995) and wild animals, including white tailed deer (*Odocoileus virginianus* - McShea et al. 1997), feral horses (*Equus caballus* - Kirkpatrick et al. 1990), and, more recently, the African elephant (*Loxodonta africana* - Fayrer-Hosken et al. 1997, Fayrer-Hosken et al. 2000, Delsink et al. 2002, Delsink et al. 2006). Southern Africa faces major concerns with rapidly increasing elephant populations in open systems as well as in many enclosed reserves and conservation areas (Slotow et al. 2005). As many of these reserves are small and enclosed by fences this could became a major problem (Garai et al. 2004, Kerley et al. 2008), to which immunocontraception offers a possible future management lifeline (Bertschinger et al. 2008).

Short-term field trials testing PZP as an immunocontraception in elephants have successfully been completed with up to 100% efficacy (Delsink et al. 2005, Delsink 2006). The immunocontraceptive vaccine is remotely delivered by drop-out darts, and therefore the darting process is quick and safe from an elephant perspective (Delsink et al. 2007). Immunocontraceptive vaccines cause an immune response, by which females produce antibodies that block the sperm receptor sites on the ovum. This prevents the sperm from attaching and penetrating the ovum after copulation, thereby preventing fertilization (Bertschinger et al. 2008). Immunocontraception is a non-hormonal contraceptive method, therefore, treated females display more frequent oestrous cycles, which vary from 12 to 18 weeks (Hodges 1998, Brown 2000). There has also been no observed effect on, or harm to, unborn calves (Fayrer-Hosken et al. 2000, Delsink 2006).

However, concerns have been raised that the increase in oestrus frequency in immunocontracepted female elephants will alter social behaviour of family groups (Kerley & Shrader 2007). It has been postulated that adult bull associations with family groups might increase and disrupt family groups, as more frequent mating attempts by adult bulls may result in adult females being harassed and physically harmed (Kerley and Shrader 2007, Perdok et al. 2007). It has also been suggested that the immunocontraception darting process might cause fragmentation of family groups, altering of bond groups or overall herd isolation (Whyte 2001).

Therefore, we tested the hypotheses that PZP immunocontraception would have social behavioural implications on treated females by assessing the influence of the actual darting application process on herd fission and fusion, determining whether herd fragmentation took place post-darting and determining the displacement and movement rates of the darted family groups. We also determined whether immunocontraception implementation within treated female resulted in an increase in the association of bulls with these family groups.

Study area

This study was conducted within the Munyawana Conservancy, KwaZulu-Natal, South Africa (27°51'30"S, 32°19'00"E). Initially Phinda Private Game Reserve (Phinda) was established in 1991, with an area of approximately 150 km^2. During August 2004, the boundary fences between Phinda and two neighbouring reserves, Zuka and Mziki Pumalanga were removed, forming the Munyawana Conservancy (185 km^2). During May 2006 the boundary fences were removed between Munyawana Conservancy and the neighbouring reserve, Sutton, increasing the area of the conservancy to 207 km^2.

The vegetation types within the Munyawana Conservancy are Sand Forest (Low and Rebelo 1996, Type 3), Sweet Lowveld Bushveld (Low and Rebelo 1996, Type 20), Natal Lowveld Bushveld (Low and Rebelo 1996, Type 26), Lebombo Arid Mountain Bushveld (Low and Rebelo 1996, Type 13) and Coastal Bushveld-Grassland (Low and Rebelo 1996, Type 23). One perennial river, the Mzinene River, flows from west to east through the southern section of the conservancy, and dams are extensively distributed throughout the properties. During the rainy season, surface water is extensive; while some of these dams retain water all year round, other dams are supplied with borehole water during the dry periods. The Munyawana Conservancy has a summer rainfall regime and temperature range from an annual mean minimum of 10 °C to an annual mean maximum of 35 °C.

Methods

Monitoring

Monitoring of the Phinda elephant population has been ongoing since March 2003. Monitoring of the populations within the newly incorporated areas began once these areas become part of the conservancy. All adult elephants were individually known through unique physical characteristics which included notches, tears and holes in ears or tusk and body configurations (as described by Moss 2001), as well as the family group demographics. In July 2006 the total elephant population within the Munyawana Conservancy consisted of 98 individuals, with 20 independent bulls and seven family groups. Of this total, the Phinda population comprised 88 individuals, with 19 independent bulls and five family groups. The Zuka population consisted of three young individuals and the Sutton elephant population comprised one family unit with seven individuals. Neither the Zuka nor the Sutton populations' amalgamated into the Phinda population once the fences were removed, i.e. there were no known associations of the different groups.

Throughout the study duration (March 2003 through to December 2007) the elephant population was monitored on a daily basis. A total of 4334 sightings during this time period were recorded and on average 20 minutes observation period was spent per sighting. As many elephants as possible were located each day, however in all instances of multiple observations of a family group in one day, only the first observation of each group was used during analyses to avoid pseudoreplication. For each observation, general location data, identities of adult individuals present and behaviour activities were recorded.

By June 2005 one female in each of the five Phinda family groups had been collared. Collar darting was done from air by helicopter (the behavioural effects of collaring are excluded from this manuscript). All sexually mature females (females with one or more calves at foot) from Phinda's five collared family groups, a total of nineteen females, were selected and contracepted on a rotational basis for the duration of the study period (see Druce et al. 2011 for methods). All the immunocontraception darting procedures during 2004 - 2007 were done from the ground, either from vehicle or on foot. Drop-out darts were used and thereafter retrieved to ensure appropriate vaccination.

Family group fission and fusion

We were interested in whether the application process of contraception darting had any influence on fission and fusion within and among Phinda's five family groups (i.e. whether the groups came together or dispersed). We compared herd fusion behaviour in periods before darting, during darting and after darting (for only the 2004 and 2005 darting events, as data collection focus shifted during further years) to determine if there were changes in the family groups' association behaviour. Association index was defined, as described by Wittemyer et al. (2005), with individuals within a 500m radius of the centre of the aggregation. Any aggregation of elephant outside this radius was defined as a separate family group. The before period consisted of the 14 days immediately before the darting process started, the during period was the actual period of darting (5 days in 2004 and 8 days in 2005) and the after period consisted of 14 days immediately after the darting process ceased. Data from 2003 were included in the analysis to determine the association behaviour of family groups a year before contraception was implemented, thus allowing comparison to behaviour during the same time of year in 2004 and 2005 (the time period each year before the onset of the contraception darting process).

We determined the response of elephant family groups to the process of contraception darting by calculating the 'grouping tendency' of each of the five family groups for each time period. This was done by calculating the total number of sightings of each family group within the given time periods, then the total number of sightings of that given family group present with other family groups were calculated. Where after the 'grouping tendency' was calculated for each family group by dividing the total number of sightings a family group associated with other family groups by the total number of sighting for that given family group for the specific time period and reflects the proportion of sightings in which that group was associated with any other family.

Two-way Repeated Measures ANOVA (RMANOVA) was used to compare association data among the different time periods (before, during and after darting) and between 2004 and 2005. Another RMANOVA was performed to determine whether grouping tendency in the 'before' period changed among the three years (2003, 2004 and 2005), with 2003 being the year before contraception was implemented.

Displacement and movement rates

We determined whether the application process of contraception darting influenced the displacement and movement rates of family groups. We analysed collar location data from 2005, 2006 and 2007; because not all collars were operational for the duration of the study, only three family groups were included for each year, and they were not necessarily the same in all three years. Due to this coarse nature of the data (only 3 of the 5 Phinda family groups), this analysis may not yield a concrete conclusion about the overall population. We excluded 2004 from the analysis because only a single herd was collared at the time of the contraception darting application. The durations of the before, during and after darting periods used in this analysis were the 14 days immediately before the darting process started, the period of darting [8 days in 2005, 9 days in 2006 (a subset from 40 day period) and 6 days in 2007] and the 14 days immediately after the darting process ceased, respectively.

Using the Animal Movement extension in ArcView 3.2, location data for each family group were used to determine the displacement distance between subsequent days and movement rates. The straight-line displacement distance per day (km/day) was calculated for each individual family group. Rate of movement was calculated using location points 12 hours apart over a multi-day period for each study group. This was calculated by dividing the straight-line distance covered by the time required to cover the distance (km/h). Due to the coarse nature of the data (time interval between subsequent location transmissions was 12 hours), our calculated movement rates are not necessarily accurate. However, this technique was used throughout this data analysis and does provide an index by which comparisons of movement in the three time periods can be made.

For both of displacement distance and movement rate, a three-way ANOVA was performed to determine differences between time periods, years and family groups. The data for both displacement and movement rates were square root transformed to meet assumptions of the ANOVA.

Bull association with family groups

We determined whether bull association with family groups increased as the number of oestrous females increased. The time frame for this analysis was from January 2003 to August 2007, with each of the five years split into four-month periods (January to April, May to August and September to December). For each four-month period, the total number of females coming into oestrus was calculated. During the time period before immunocontraception was implemented (i.e. Jan 2003 to May 2004), the occurrence of oestrus for each female was calculated by subtracting 22 months (length of gestation) from the month of the birth of her calf (Wittemyer et al. 2005). After the implementation of contraception (May 2004 to August 2007), we calculated when each female would be in oestrus by adding 16 weeks to the date of birth of her last calf to give the approximate date of her first oestrous cycle after contraception taken effect. Subsequent oestrous cycles for each female were determined by adding 16 weeks to the date of each calculated oestrous cycle thereafter. A 16 week oestrous cycle was chosen as Hodges (1998) and Brown (2000) indicated oestrous cycle length varied between 12 to 18 weeks. This was determined for each female which enable us to calculate how many females within each family group would have been in oestrus during each four month period. No behavioural or physiological methods were used to determine oestrus females in this study, due to the nature of the dense habitat, we could not observe the oestrous cycles within all females. With a degree of uncertainty we are aware that there might be a large variation within the oestrus analysis, however we do not expect the variation to push the results in any particular direction. We believe it is reasonable to use this analysis as a form of an average at the population level in order to generate some form of understanding of degree of cycling within female population. In order to determine association of bulls with family groups, observation location data were used within each four month period and for each of the five family groups. All location data were filtered per family group and the total number of sightings per four-month time period was calculated. Thereafter, from the subset the percentage was calculated for which adult bulls were present with the family group sightings. An adult bull, for this analysis, was defined as any sexually mature bull older than 15 years of age (Hanks 1972, Bertschinger et al. 2008) that moved independently of its natal family group. Two of the 20 bulls were younger than 22 years of age, the other 18 bulls were between 22 and 44 years of age.

Simple linear and polynomial regression analyses were performed to evaluate the relationship between bull association with family groups and the number of oestrous females, for each family group. To prevent an accumulation of Type 1 errors leading to a potentially false conclusion about the prevalence of a significant relationship when multiple groups were evaluated, we Bonferroni-adjusted the critical p (0.05/5 = 0.01) before making statistical conclusions from the regression results.

All statistical analyses were performed using SPSS (v. 11.5 and 15.0), using alpha of 0.05. For the regression analysis the Bonferroni-adjustment was critical alpha of 0.01. Assumptions for the regression and all ANOVAs were tested and satisfied.

Results

The immunocontraception darting team observed some avoidance behaviour from the elephant family groups towards them; this avoidance seemed specific to the darting team and not to general human activities. Family groups were observed to sometimes move hurriedly short distance away from the actual darting position, before settling down again. All these observations were very sudden, subtle and short-lived, that none of these observed reactions by family groups during the actual darting process were detected in the statistical analysis as included below.

Family group fission and fusion

Two-way Repeated Measures ANOVA (RMANOVA) was performed to determine whether grouping tendency was affected by the process of contraception darting for 2004 and 2005 (Table 1). There were no significant differences in grouping tendency among the before, during and after darting periods ($F_{0.05\,(2),\,2,\,16}$ = 2.409; P = 0.122). , or between years ($F_{0.05\,(2),1,8}$ = 0.752; P = 0.411). Additionally, there was no interaction between time period and year ($F_{0.05\,(2),2,16}$ = 0.024; P = 0.976).

Another RMANOVA was used to evaluate differences in grouping tendencies in the before darting period comparison among three years (2003, 2004, 2005). There was no significant difference in grouping tendencies ($F_{0.05\,(2),\,2,\,8}$ = 0.708; P = 0.521) between the three years.

Displacement and movement rates

Differences in displacement distances and movement rates, for collared family groups for the periods directly before, during and directly after contraception darting in 2005, 2006 and 2007, were evaluated using three-way ANOVAs. Neither the displacement distance over consecutive 24-hour periods nor movement rates were significantly affected by any of the factors in the model ($p > 0.05$; Table 2). However, the movement rate model showed a tendency towards the variable year ($p = 0.073$).

Bull association with family groups

The relationship between association of bulls with family groups and the number of oestrous females in family groups was evaluated with regression analysis for each group. There was no observed trend for bull association to increase with number of oestrous females (Table 3), and, in fact, none of the family groups showed a significant relationship between bull association and number of oestrous females in the group, using a Bonferroni-adjusted critical p value (Table 3). This lack of apparent relationship, along with the presence of high variability in bull association for any value of number of oestrous females, was also illustrated when all family groups were combined in one scatterplot (Fig.1). Even with zero females in oestrus there was a 30% to 91% bull association with the family groups (Fig. 1), which indicate a huge variation within male association.

Table 1. The effect of contraception darting on the individual family groups' fission and fusion dynamics, represented as the proportion that each herd was seen with other family groups out of the total number of sightings for that family group during the given time periods. As the value tends to zero, the family group was increasingly alone.

Family Group Code	**2003**	**2004**			**2005**		
	14-day period[1]	14-days before darting	5-days during darting	14-days after darting	14-days before darting	8-days during darting	14-days after darting
FG1	1	0	0.67	0.75	0	0	1
FG2	0.25	0	0	0.44	0.5	1	1
FG3	0.50	0.33	0.5	0.67	0.33	1	0.33
FG4	0.50	0	1	0.60	0.50	0.50	0.60
FG5	0.40	1	0.33	0.63	0.67	0.33	0.67

[1]This period is the same time of year as the before periods in 2004 and 2005.

Table 2. Results of 3-way ANOVAs, testing for differences in displacement distance (km.day^{-1}) or movement rate (km.hr^{-1}) among family groups (N = 3 groups per year, not always the same groups), darting period (N = 3; before contraception darting period, during contraception darting period, and after contraception darting period), and years (N= 3 years; 2005, 2006, 2007). Displacement distance and movement rates were square-root transformed.

Dependent variable	Model term	F	df	p
Displacement distance	**Family group (FG)**	1.627	4	0.394
	Darting period (DP)	0.150	2	0.964
	Year (Y)	0.620	2	0.619
	FG * DP	1.363	8	0.399
	FG* Y	2.031	2	0.235
	DP * Y	1.931	4	0.274
	FG * DP * Y	0.828	4	0.508
Movement rate	**Family group**	1.368	4	0.430
	Darting period	0.492	2	0.630
	Year	17.929	2	0.073
	FG * DP	2.078	8	0.227
	FG* Y	0.311	2	0.747
	DP * Y	3.414	4	0.133
	FG * DP * Y	0.665	4	0.616

Table 3. Results from regression analyses of the relationship between bull association with family groups and the number of oestrous females, in four-month periods, for each of the five family groups. R^2 and p are presented from the best model for each family group. N = 14 four-month periods from 2003 to 2007, for each family group.

Family Group	Number of oestrous females (range)	R^2	P [1]	Number of oestrous females at which maximum bull association was observed
FG1	0-5	0.024	0.595	3
FG2	0-3	0.008	0.756	3
FG3	0-6	0.111	0.244	1
FG4	0-2	0.004	0.826	1
FG5	0-3	0.010	0.740	3

[1] Bonferroni-adjusted critical p = 0.01

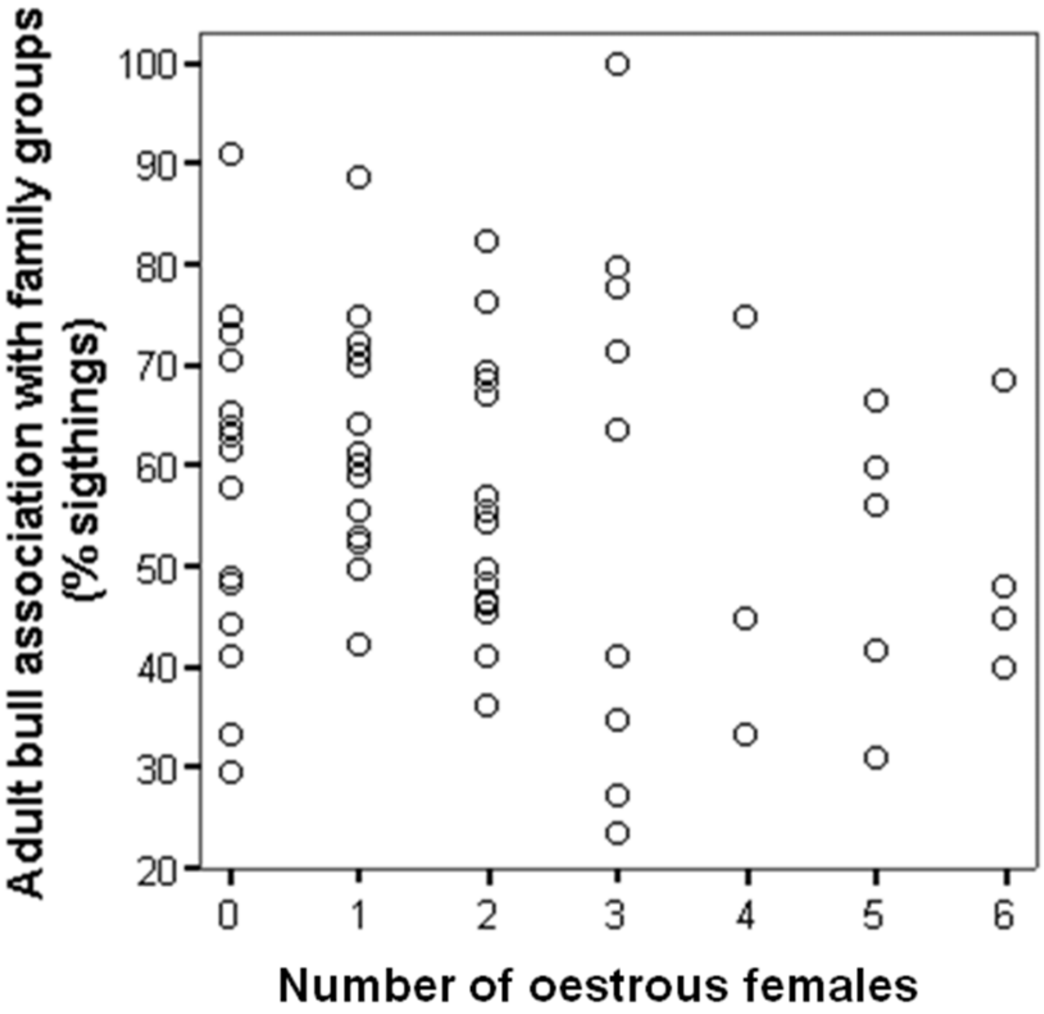

Figure 1. The relationship between adult bull association with family groups (% of sightings where adult bulls were present with family groups) and the number of oestrous females in a four-month period (N = 14 periods).

Discussion

We used behavioural monitoring to determine the consequences and effects of the management intervention of immunocontraception on elephant family groups. Overall, there was no significant disruption in behaviour from implementation of immunocontraception darting on the breeding female population. If there were a behavioural response of elephants to the darting process, we would have expected to notice a social response, with herds grouping together more [e.g. response to female immobilisation (Burke 2005), poaching (Andersen and Eltringham 1997) or catastrophic fire (Woolley et al. 2008)]. In another study of the implementation of contraception in elephants, there was also no fusion tendency, but other elephants showed a tendency to fragment more over time as the population aged and increased (Delsink 2006). The latter findings are similar to the observed behavioural responses of our family groups: no herd congregation was observed, while a subsequent, small decrease in association over time was indicated, probably as a consequence of maturation of the young population (pers. obs.).

Several other studies (Pretorius 2004, Burke 2005, Douglas-Hamilton et al. 2005) have indicated a significant increased mobility when elephants experience human-induced disturbance. When darted from the ground (as opposed to from a helicopter) family groups moved away from the darting team, and core ranges shifted over the darting period (Delsink 2006). Although some avoidance behaviour was observed from the Phinda elephant population during the immunocontraception administration process, there was no significant change in mobility within family groups before, during and after the annual darting procedure, indicating no detected behavioural response. One of Munyawana's main objectives is eco-tourism, and there was no observed effect of the implementation of immunocontraception on safari activities and sightings (pers. obs.).

Concerns about the use of immunocontraception causing an increase in bull association with contracepted females that come into oestrus more frequently (Kerley and Shrader 2007) were not supported by our study. Rather, we observed no relationship between number of oestrous females in a group and bull association with that group, as found by other studies (Whyte and Grobler 1998, Delsink et al. 2002, Delsink et al. 2006). Therefore, the increased frequency of females coming into oestrus with the use of immunocontraception does not result in an increase of bull association with family groups. Regardless of the large variation within the data, it was a reasonable measure to use for an average at the population level in order to generate some form of understanding of degree of cycling within the female population.

Although we are confident that there is no short-term effect on contracepted elephant females, longer-term monitoring studies are essential to determine whether immunocontraception may have long-term behavioural consequences. Current data suggest there is no increase in the number of bulls associating with family groups containing one or more contracepted females, which come into oestrus more frequently; however, it may also be valuable to look at longer-term association patterns (Delsink 2006, Bertschinger et al. 2008 and this study). The prevention of conception in individual females for prolonged periods of time, as well as consecutive abnormally long calving intervals, may affect social and maternal behavioural in the long-term and thus need to be evaluated (Bertschinger et al. 2008). Due to elephants being such long-lived creatures it might take many years for long-term changes or effects to be detected, but in the short- and medium-term immunocontraception appears to have no significant social or behavioural effects (Delsink et al. 2007) at both the individual and population level when used on a rotational basis.

Immunocontraception has been demonstrated to be a practical, non-disruptive, non-lethal population control method (Delsink 2006, Delsink et al. 2006, 2007, Bertschinger et al. 2008 and this study). As immunocontraception can be applied successfully to restrict population growth rates in a long-lived, socially complex species, such as elephants, with negligible behavioural and social effects, it could be effective for population control in other socially complex or long-lived wildlife species. Managers of conservation areas, especially small, enclosed reserves should consider immunocontraception as a viable, effective and adaptive management tool.

CHAPTER 7

THE EFFECT OF MANAGMENT INTERVENTIONS ON ELEPHANT ASSAYED AT THE POPULATION AND BREEDING GROUP LEVELS.

Abstract

Socially-complex, gregarious, long-lived animals are sensitive to disruption of their social dynamics. However, within restricted protected areas, management intervention of such sensitive species might be required. Understanding of these species' social behaviour is essential for efficient management interventions with the least impact and most effective results. We determined the effect of management interventions on elephant behaviour within Munyawana Conservancy and Pilanesberg National Park, South Africa. The management interventions assessed were female and male GSM/GPS satellite collaring, female immunocontraception, culling or hunting of males, and family group live removals. The populations' breeding group group-size was not affected by season, rainfall or management interventions. The mean distance between herds was not affected by management intervention. Socially-complex species respond to human interventions, however different populations might react differently to human induced stress though management events. Conservation management should therefore consider management interventions for the intended scenario with the most effective predicted outcome, but with the lowest holistic impact.

Key words: sensitivity assessment, management intervention assessment, Munyawana Conservancy, Pilanesberg National Park

Introduction

Socially-complex, gregarious, long-lived animals are sensitive to disruption of their social dynamics. In killer (*Orcinus orca*) and humpback whale (*Megaptera novaeangliae*), along with bottlenose dolphin (*Tursiops truncatus*), short-term behavioural changes, such as avoidance or aggressive displacement behaviour towards tourism boats (Williams et al. 2002, Lusseau 2004, Hawkins and Gartside 2009), might affect their breeding, social and feeding behaviour (Weinrich and Corbelli 2009). Bottlenose dolphin abundance declined within tourist areas, as long-term displacement away from these disturbed areas (Bejder et al. 2006). High levels of human disturbance, such as habitat destruction and poaching, have long-term impacts on mountain gorilla (*Gorilla gorilla*) (Robbins et al. 2009). During the 18th to 20th century in the United States, grey wolf (*Canis lupus*) were persecuted, resulting in vast within population disruptions of social structure (Weiss et al. 2007). In more recent years, habitat fragmentation, road kill and poaching have been the main causes of social and population disruption of grey wolf (Blanco and Cortes 2007, Lovari et al. 2007). African elephant (*Loxodonta africana*) social grouping may change when elephant are under management intervention pressure (e.g. hunting (Burke et al. 2008); female immobilisation (Burke 2005)), poaching (Andersen and Eltringham 1997, Owens and Owens 2009), or from catastrophic arson fire (Woolley et al. 2008b)). Sustained pressure, for example, in response to poaching, may result in disruptions within population demographic social structure and mating success over the long term (Bradshaw et al. 2005, Gobush et al. 2008, Ishengoma et al. 2008). Social species often show a response to external stressors (Lusseau 2007; Parson et al. 2009). Therefore, management interventions may pose a risk of possible consequences from ecological, social and welfare perspectives.

Wildlife management and decision-making needs to take into account the ecological processes of ecosystems and its biodiversity, the socio-political and economical values (Biggs et al. 2008), especially with a socially-complex, gregarious, long-lived species like elephants (Douglas-Hamilton and Douglas-Hamilton 1975, Moss and Poole 1983, Slotow et al. 2005). Conservation management should therefore consider management interventions for the intended scenario with the predicted most effective outcome, but with the least holistic impact (Sukumar 2003). However, any management strategy or intervention might have a potential uncertain, unforeseen risk component (Slotow et al. 2008). It is important to incorporate social structure and behaviour into risk assessment of interventions and management decision-making to accurately evaluate the persistence of social species and the influence of human interventions (Parson et al. 2009). This understanding and knowledge of behaviour is then essential for developing tools that are required for the most effective management of the species with the least negative impact (Singh and Kaumanns 2005).

Elephant society is a female dominant social hierarchy, with the oldest, largest female (the matriarch) dominating and leading the family group (Archie et al. 2006). Older matriarchs have greater social knowledge, and are more confident in leading their family groups, and respond more appropriate to risky situations (McComb et al. 2001, 2011). Within young orphan, re-introduced elephant populations in South Africa (see Slotow et al. 2005), females are 'forced' into a matriarchal role at a very young age, due to the lack of any older introduced females (similar to poached populations, see Owens and Owens 2009). Due to the fast population growth rate within these populations (Garai et al. 2004, Slotow et al. 2005, Mackey et al. 2006), family groups may increase in numbers very rapidly, and may split, resulting in another young inexperienced matriarch leading the splinter group (as in Bradshaw et al. 2005). Management of these orphan introduced elephant populations is essential, as most of these populations are within small, enclosed reserves with initially unstable social structures, and consequential dangerous behaviour (Slotow et al. 2000, Slotow et al. 2008). It is essential to determine the influence of management intervention, and to apply management tools that assist in stabilizing these eruptive, young populations, or that may be required for ecological reasons (Garai et al. 2004, Slotow et al. 2005).

We therefore aimed to determine the effect of direct management intervention on elephant within a small, enclosed reserve through interpretation of social behavioural. Our specific objectives were to determine if (1) breeding group size and (2) distance between breeding groups, changed during different management interventions within the Munyawana Conservancy population. As the assays used appear not to detect any significant effects within the first study site, a second study site, Pilanesberg National Park, where behavioural responses had been detected (Burke et al. 2008, Woolley et al. 2008b), was reassessed using these assays.

Study Areas

This study was conducted firstly within the Munyawana Conservancy (MC), located in KwaZulu-Natal, South Africa (27°92' - 27°68' S and 32°44' - 32°20' E). Initially Phinda Private Game Reserve (Phinda) was established in 1991, with an area of approximately 150 km^2 (Druce et al. 2006a). During August 2004, the boundary fences between Phinda and two neighbouring reserves, Zuka and Mziki Pumalanga were removed, forming the Munyawana Conservancy (185 km^2). During May 2006 the boundary fences were removed between Munyawana

Conservancy and the neighbouring reserve, Sutton, increasing the area of the conservancy to 207 km^2. According to Mucina and Rutherford (2006) the vegetation types within the Munyawana Conservancy are Sand Forest, Southern Lebombo Bushveld, Zululand Lowveld, Western Maputaland Clay Bushveld, Makatini Clay Thicket, Maputaland Coastal Belt and Subtropical Salt Pans. One perennial river, the Mzinene River, flows from west to east through the southern section of the conservancy, and dams are extensively distributed throughout the properties. During the rainy season, surface water is extensive; and while some of these dams retain water all year round, other dams are supplied with borehole water during the dry periods (Druce et al. 2006b). The Munyawana Conservancy has a summer rainfall regime, with annual rainfall ranging from 350 mm to 1100 mm, and temperature ranging from an annual mean minimum of 10 °C to an annual mean maximum of 35 °C. During 1992-1994, 54 elephant were introduced (Druce et al. 2008), with an additional three mature adult bulls in 2003 (Druce et al. 2006b). By 2003 the Phinda population reached 110, and in June/July 2003, 37 elephant comprising four different family groups were translocated from Phinda (Druce et al. 2008). By July 2006 the total population within the Munyawana Conservancy consisted of 98 individually identified elephant, with 20 independent bulls and seven breeding groups. Of this total, the Phinda population comprised 88 individuals, with 19 independent bulls and five breeding groups. The Zuka population consisted of three young individuals and the Sutton elephant population comprised one family unit with seven individuals. Neither the Zuka nor the Sutton populations' amalgamated into the Phinda population and consequently were not included in this study.

Secondly, Pilanesberg National Park (PNP) is located in North West Province, South Africa (25°8' - 25°22' S and 26°57' - 27°13' E). The reserve was established in 1979, with an area of approximately 500 km^2 and later increased to 570 km^2 by the end of 2008. The park is circular in shape, is located in the crater of an extinct volcano, and as such has hilly savanna relief (Burke 2005). The park falls within the transition zone that lies between the Kalahari Thornveld in the west and the Bushveld in the east. The habitat type is classified as sourveld, dominated by Acacia and broad-leaf bushveld growing on rocky mountains and hills. The habitat ranges from closed thickets to open grasslands (Acocks 1988). The park consists of one major river system running through the centre, various ephemeral tributaries and pumped water points are distributed throughout the reserve, with one large central dam. The annual rainfall is 630 mm with a range of 480 mm to 1000 mm, which falls mainly in the summer, and temperatures range from an annual mean minimum of 5 °C to an annual mean maximum of 31 °C. During 1979–1998, 95 elephants were introduced. Fourteen of the males were culled and a further 15 elephants died between 1979 and 2001 of other causes (Slotow and van Dyk 2001). By September 2005, the PNP population totalled 165 individually identified elephants, of which 37 were independent adult bulls and 128 were part of 18 relatively stable matriarchal breeding groups (Woolley et al. 2008).

Methods

We investigated the short-term social behavioural responses of elephant to various management interventions within the study area. The time period used in analyses to determine the response to management interventions were 14-days periods immediately before and after interventions took place (analogous to Burke et al. 2008, short-term immediate response period).
All statistical analyses in this manuscript were performed in SPSS (v. 15.0) with alpha of 0.05. In the case of parametric tests, all assumptions were tested and satisfied.

Breeding group size

Previous studies have indicated that breeding groups amalgamate together during human interventions (e.g. response to female immobilisation (Burke 2005), poaching (Andersen and Eltringham 1997) or catastrophic fire (Woolley et al. 2008b)). We therefore wanted to determine if management interventions influenced breeding group size within our two study populations. We also assessed environmental factors (Western and Lindsay 1984) (season and monthly rainfall), to establish their influence on the breeding group size. The elephant population was monitored daily and as many elephant as possible were located each day. All the adult individuals were known through unique physical characteristics, and individuals present were recorded at each sighting. At the first sighting for each herd per day, we recorded the total group number of individuals present; where more than one breeding group was located together, this combined group size reflected the sighting for the day for all breeding groups involved (population demographic is known within both reserves; i.e. adult individuals are identified and breeding group associations are known). All data points of elephant at waterholes were excluded from these analyses, as elephant are frequent found to congregate at water resource points (Stokke and du Toit 2002). The mean group size was calculated for each time period [MC: the average N (= number of sightings per intervention) before = 13.5, after = 16.7; PNP: the average N (= number of sightings per intervention) before = 13.6, after = 13.9].

We determined the response of elephant group size to seasonal changes for the two year time period (MC: April 2003 to April 2005, and PNP: March 2002 to March 2004). Group size was calculated separately for summer (wet) and winter (dry) seasons. The length of a season was defined by the rainfall of that year, with the wet summer beginning 10 days after >15 mm of rain in September/October. Dry winter began when there had been no significant rainfall (<15 mm) for two weeks after 15 March, to as late as mid May. We used the coefficient of variation of the group size per each season as a measure of variability in grouping behaviour, and determined if breeding group size was affected by season (summer and winter) over the two years for each reserve using an independent T-test on the coefficient of variation (CV is used due to the small magnitude of the data). As the response of the environment to rainfall is not instant due to the lag between rainfall and the onset of new leaf growth (Shannon et al. 2010), the preceding month's rainfall was used with the current month's group size data during both the seasonal and monthly rainfall (analysis below) analyses. We aimed to determine if there was a lag response in group size to seasonal effects.

To determine if group size was affected by monthly rainfall, the same two year study period for both reserves were used. A linear regression analysis was performed for the preceding month's rainfall (i.e. lag-rainfall response) to determine the relationship between group size and rainfall.

To determine if management interventions influenced breeding group size, the mean group size was calculated for a 14-day time period before and after each intervention (see Table 1 for interventions). A paired sample T-test was performed for each reserve to determine if the breeding group size was affected by management interventions.

Distance between breeding groups during management interventions

To determine if the social grouping among breeding groups were affected by management interventions, the distance between breeding groups was calculated. Only adult female GSM/GPS satellite collar data were used during this analysis, as daily data points were recorded at predetermined time intervals. Only the first data point after 07h00 for each collared female was used, with data points for all females < 6 h apart on any day. Data were only analysed for time periods where there were at least three females from different groups collared at the same time. We measured the daily straight-line distances between each breeding group and for each day, calculated the mean of these distances. We then calculated the mean distance for each 14-day period before and after each management intervention. A Wilcoxon paired-sample test was performed to determine if the distance between breeding groups were affected by management interventions. Thereafter all the management interventions were grouped into events relating to either male or female based interventions. These female and male data sets were analysed separately using a Wilcoxon paired-sample test to establish whether the distances between breeding groups during different management interventions for each reserve were significantly different for male and female based interventions (see Table 1 for event types).

Results

Seasonal changes had no significant effect on breeding group size within MC (t_3 = -1.314, P = 0.880) or within PNP (t_3 = -0.030, P = 0.427). There was no significant effect of lag monthly rainfall response on breeding group size for either MC (linear regression $F_{1,23}$ = 0.019, P = 0.891) or PNP (linear regression $F_{1,20}$ = 1.224, P = 0.282). With high rainfall (i.e. during the wet season months) there was a lower variability in group size than during the dry winter months (Fig. 1). Because of the relatively small influence of these environmental proxies, we did not account for environmental differences when contrasting among interventions.

Paired sample T-tests were performed to determine if management interventions had an effect on breeding group size. Management interventions had no significant effect on group size, neither in MC (t_{11} = 0.603, P = 0.559) nor PNP (t_7 = 0.855, P = 0.421).

Management interventions had no significant effect on the distance among breeding groups (Fig. 2), neither in MC (Wilcoxon paired-sample tests Z = 0.459; P = 0.646) nor PNP (Wilcoxon paired-sample tests Z = -0.280; P = 0.779). Thereafter, additional Wilcoxon paired-sample tests were performed to determine whether the social grouping between breeding groups was affected by different male and female management interventions. Within the MC population with only female management interventions included, there were no significant differences in distance between breeding groups (Z = -0.169; P = 0.866), additionally with male only management intervention no significant difference were found (Z= -0.535; P = 0.593). Within the PNP population with only female management interventions included, there were no significant differences in distance between breeding groups (Z = -0.135; P = 0.893), nor between male only management interventions (Z = -0.535; P = 0.593).

Table 1. List of the management interventions within both conservation area used for this study.

Munyawana Conservancy		
Management Intervention	**Date**	**Analysis used**
Family Group Live Removal	6-16 Jun 2003 8 Nov 2007	1 2
Male Collaring	20 Jan 2004 3 Nov 2004	1 1, 2
Female Collaring	20 Oct 2003 15 Jul 2004 16 Jul 2004 20 Jul 2004 16 Jun 2005 12 May 2006 21 Oct 2006 26 Oct 2006 25 Jan 2007 2 Mar 2007 21 Jun 2007 13 Sept 2007	1 1 1 1 1 1, 2 1, 2 1, 2 1 2 2 2
Female Immunocontraception Darting	28-30 May 2004 26-30 Jun 2004 14-21 Jul 2004 6-16 Jun 2005 6 May-14 Jun 2006 17-22 Jun 2007	1 1 1 1 1, 2 2
Male Cull	31 Oct 2006 8 May 2007	2 2
Female Sterilization Operation	16, 20 Jun 2004	1
Female Sterilization Re-examination scan	16 Jun 2005	1

Pilanesberg National Park		
Management Intervention	**Date**	**Analysis used**
Male Hunting	16 Apr 2002 30 Jul 2002 9 May 2003 7 Aug 2003 13-14 Aug 2004 22-23 Jul 2005	1 1 1 1 2 2
Female Collaring	17-19 Sep 2002 20-21 Oct 2004 22 Feb 2005 28 Oct 2005	1 1 2 1, 2
Euthanising	23-24,27 Sep 2005 7 Oct 2005 28 Oct 2005 10, 14 Nov 2005	2 2 1, 2 1, 2

Analysis used: [1] Breeding group size analysis (only visual sightings data used)
[2] Distance between breeding groups analysis (only collar data used)

Definitions:

1. Family Group Removal - the process when a family group is capture, removed and translocation from the resident population/reserve and released into a new area.
2. Collaring - the process when an elephant is immobilised to fit a VHF or GMS/GPS satellite collar around the neck of the individual.
3. Immunocontraception Darting - a method to administered the immunocontraception vaccine by a drop-out dart, darting on foot or from vehicle. The vaccine causes an elephant's immune response to reduce fertility by controlling or preventing conception and pregnancy.
4. Culling - the process when an elephant is killed/destroyed by management due to management or authority reasons.
5. Hunting - the process when an elephant is killed/destroyed by a hunter and generally funds are generated through this process.
6. Euthanising - the process of killing/destroying an elephant due to the severity and irreversibility of injuries (e.g. PNP a severe field fire burned some elephants).
7. Sterilization - the surgical process where the fallopian tubes of a female elephant is tied off to prevent any further reproduction.

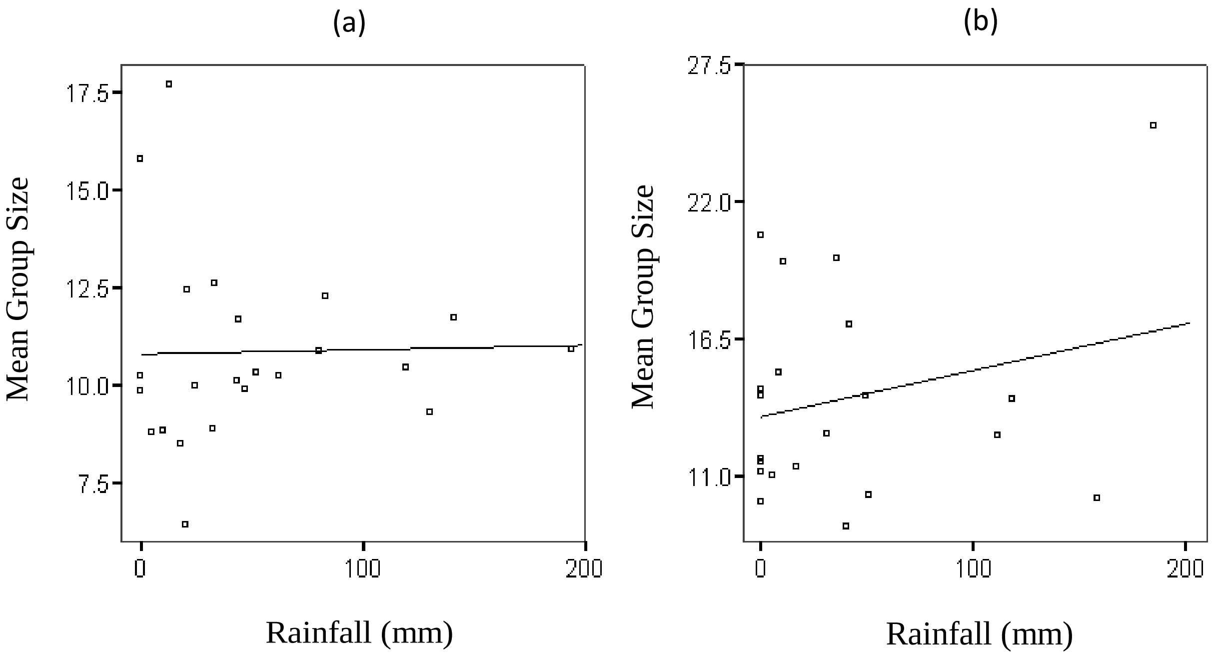

Figure 1. The relationship between rainfall and mean group size for (a) the MC population from April 2003 to April 2005 and (b) PNP population from March 2002 to March 2004. Both figures use rainfall from the preceding month to account for the lag in vegetation growth responses.

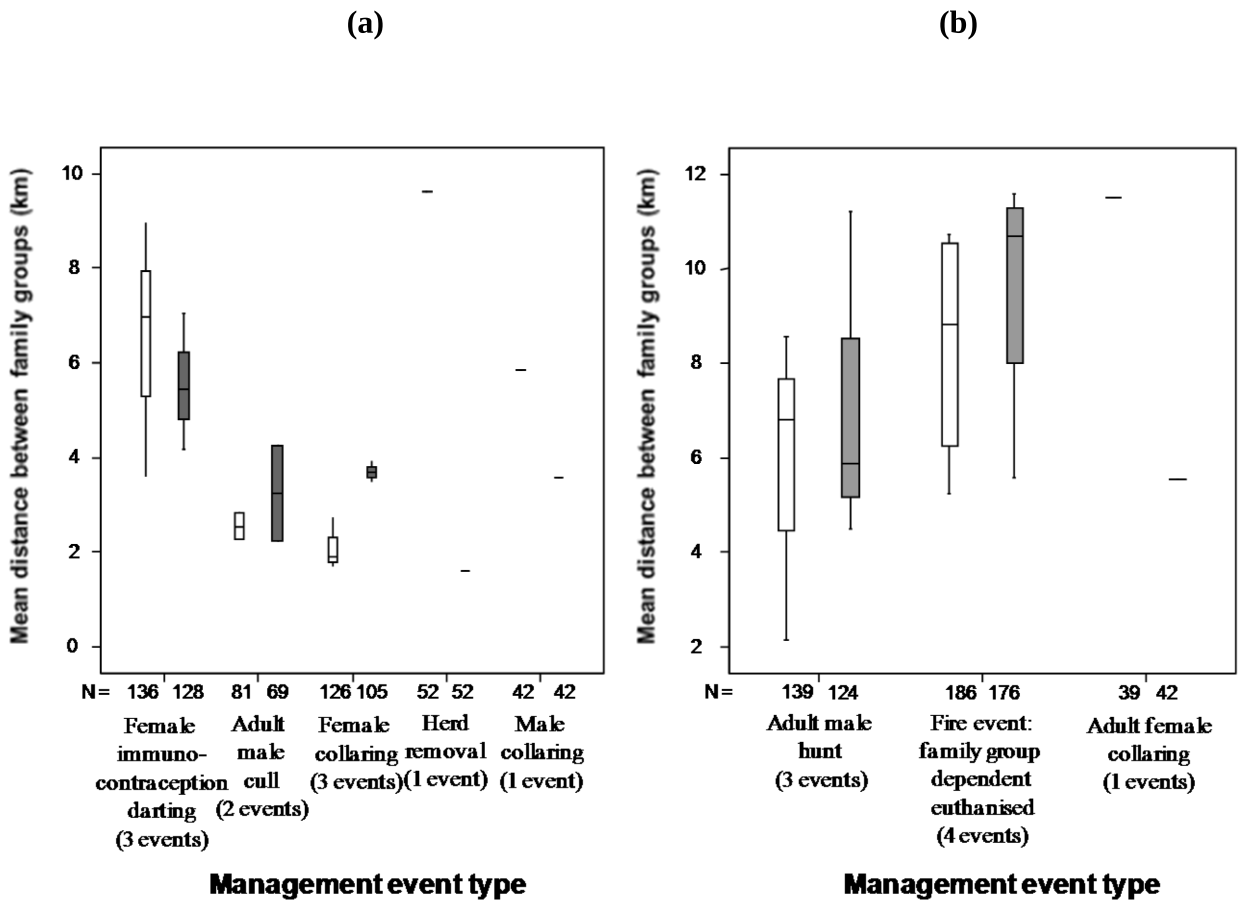

Figure 2. The mean distance between breeding groups before (white) and after (grey) different management event types were indicated for (a) the MC population and (b) PNP population. The number that N refers to is the total sample size of each event for the time period before and after.

Discussion

With a complex social species, one might expect to detect some social behavioural changes during human intervention and disturbance. Other studies have indicated that breeding groups amalgamate together during human interventions (e.g. response to female immobilisation (Burke 2005), poaching (Andersen and Eltringham 1997) or catastrophic fire (Woolley et al. 2008b)).

This study indicates that the two behavioural measures analysed (breeding group size and distance between breeding groups) had no significant response to human interventions. However, other studies have shown a reaction from elephants to interventions (Anderson and Eltringham 1997, Burke 2005, Woolley et al. 2008b). Different populations may respond differently to human induced stress during interventions, possibly as a result of the density of the population, the frequency of interventions or the intensity of interventions. In this study, the first study site (MC) showed no behavioural response. Thereafter, a second study site (PNP) was assessed, as other studies (Burke et al. 2008, Woolley et al. 2008b) had detected a behavioural response this population to human interventions. However, we used different behavioural assays to those of previous studies, but assays which the literature suggested should show response to disturbance, and no behavioural response was found.

Therefore, it is important to use the correct range of indices as behavioural assays to determine if the intervention have an impact on the elephant populations. Sometime sociality behavioural assays such as group size and distance between herds, may not always be the best indexes to use (this manuscript, Druce et al. 2006a, Druce et al. under review), but spatial and movement assays (Druce et al. 2006b, Druce et al. 2008, Druce et al. under review, Vanak et al. 2010) might be more appropriate indexes to detect a response. Unfortunately, we did not have enough data around the interventions to assess using such assays. A more sensitive assay which could be used to measure the response to human interventions is physiological hormonal analysis (as in Burke et al. 2008, Woolley et al. 2008b). The behavioural and physiological impact assessment typically emphasizes immediate response to human activity, but the biological relevance is rarely known (Bejder et al. 2006). Therefore an understanding and knowledge of these species social behaviour over time is essential, so that a response is not only quantified within a snap shot analysis and with a limited array of assays. However, social behaviour is only an indicator of the risk of management interventions and not a measure of its impact.

Within enclosed conservation areas, management of long-lived, complex-social species might be essential. However the most effective management intervention, which causes the least social impact and occurs within the shortest possible time (Singh and Kaumanns 2005), should be used. Generally when no significant behavioural response was detected within a study, it indicates that the effect of the interventions tested within these populations was relatively small, and will be a low welfare risk. However, as not all behavioural assays may detect a response. It is therefore important consideration when monitoring the effects of management on complex social species, that provision is made to collect the correct information, which will allow more sensitive assays to be used. These include especially small scale movement data (e.g. Druce et al. 2006b, Vanak et al. 2010), or cortisol levels in dung (e.g. Burke et al. 2008, Woolley et al. 2008b). Such data would be valuable in assessing both the risk of interventions, as well as their effects on the welfare of animals involved.

CHAPTER 8
GENERAL CONCLUSION

Strategies used to manage elephants are extremely controversial. This is largely due to the perception that elephants modify their habitat (Cumming et al. 1997) and threaten biodiversity (Cumming et al. 1997, Lombard et al. 2001, Wiseman et al. 2004). This has resulted in conflict arising between conservation and management objectives with regard to the biodiversity protection of conservation areas and the fact that elephants are a socially-complex, long-lived species which still have huge public appeal (Sonnekus and Breytenbach 2001). In addition, they are on the rare and endangered list (Reynolds and Braithwaite 2001). Extensive negative publicity and ethical concerns have been raised from previous culling and translocation procedures (Lecocq 1997) as they were perceived to be inhumane. It is important to determine the public perspective and ethical concerns relating to management of animals within protected areas (Fennell 1999), but at the same time it is necessary to educate the public about the need to manage enclosed populations and to inform them of the limitation in management options, especially for elephants. Management is defined as the manipulation or skilful handling of a resource that usually involves some form of active manipulation of the biota (Spinage 1979) and must ultimately be based on a series of assumptions given the best available knowledge (Whitehouse and Kerley 2002).

Because of these conflicts and in order to integrate science and best available knowledge into management decisions, various publications have been completed in South Africa over the past few years (for example Owen-Smith et al. 2006, Biggs et al. 2008). This knowledge was used to produce the National Norms and Standards for the management of elephants in South Africa which outlines all the options available to managers of elephant populations. However, because each conservation area management has different objectives, managers need to determine which interventions or combination of interventions would best suit their conservation areas' needs. Part of their decisions would be based on the predicted effect of the intervention on the elephant population. Consequently, the broad aims of this study were to determine the influence and effect of certain management interventions on the resident elephant population within the Munyawana Conservancy (MC) and Pilanesberg National Park (PNP). Of the array of interventions catered for in the National Norms and Standards for the management of elephants in South Africa, the following were implemented, monitored and analysed in this thesis: mature bull introduction, conservation area expansion and immunocontraception.

Three mature bulls were introduced into the Munyawana Conservancy in an attempt to normalise the bull population age structure and to reduce the abnormally long musth period of one particular resident bull. The mature bull introduction appeared successful, with all the introduced bulls coming into musth within 11 months after introduction. There was no immediate change within the oldest resident bull's musth duration or behaviour, however over time changes were observed. The bull introduction had no effect on the ranging patterns of the resident bulls however; there might have been a slight season response. The introduced bulls settled into restricted ranges separate from the family groups. There was a quick, subtle effect on the resident bull group size immediately after the introduction whereby the resident bull group size decreased immediately and the retuned to previous average size. In Pilanesberg National Park (with a similar bull scenario), the abnormal musth duration and aberrant behaviour of young resident bulls were almost instantly corrected after the introduction of older bulls and after culling certain problem resident animals (Slotow et al. 2000). The Munyawana Conservancy's resident bull population responded only with subtle changes to the introduction and there was no removal of other bulls from the population. Consequently we conclude that future bull introductions will be successful in other populations, but if a rapid solution is required in worst case scenarios, it might be essential to consider the removal of the problem animals from the population to ensure immediate success. This may also assist in normalising population structures in populations containing a large number of younger bulls.

This study also showed that conservation area expansion through the removal of boundary fences between reserves might be the least invasive management intervention, although the reaction time of the elephant population is much slower than any of the other interventions studied. With management actions such as culling and translocation, the density of individuals is lowered immediately within the area of operation. However, with fence removal, the land area is increased and therefore the density per hectare is lowered, but the area utilised remains the same initially, due to the slow response of elephants in moving into the new area. During the area expansion in the Munyawana Conservancy, the elephants appeared to perceive the new unexplored area as a threat, although this threat was reduced with time as they became more familiar with the new area. The spatial scale of response of the elephants was relatively small, while the temporal scale of response was relatively large. Due to the slow response of elephants to area expansion, it is important to implement it as a management option in advance, before the elephant density is too high for a particular area. It may be an option to use immunocontraception to reduce the population growth rate while looking to increase the size of the conservation area. As contraception only takes effect in the medium and long term, it is, therefore, not a solution to reduce an already overpopulated area, nor can it slow growth rate immediately after the first application. The use of contraception as a management tool slows growth rate over time and therefore allows more time to deal with the overpopulation issue through land expansion and, furthermore, allows time for the elephants to accept, settle into and utilize the new area.

In this study, rotational immunocontraception was successfully used to maintain a low elephant population growth rate. The process of immunocontraception application had no significant effect on herd association nor on displacement distance and movement rates. The results of the study indicate that rotational immunocontraception could be used as a realistic, safe and reversible elephant population management tool even in small-enclosed areas where eco-tourism is one of the main objectives. Large reserves with high elephant population densities may also be able to consider immunocontraception as a management option using the 'mass-darting approach'. By aiming to contracept a certain percentage of the female population annually, they will still be able to ensure a slower population growth rate. Already overpopulated and still increasing elephant populations in conservation areas, can be reduced initially by conservation area expansion, translocation or culling followed by the use of immunocontraception to maintain a low future population growth rate. Alternatively, for a more extreme effect, a contraception rate of 100% over a long term would result in no calves being added to the population. Consequently the population would age, due to the average age of individuals in the population increasing over time. If this rate were applied over an even longer time period, the population size would decrease through senescence without births, a possible alternative to culling. However, behavioural effects of this intensity of immunocontraception would need to be determined as there have been suggestions that there could be negative responses (Kerley and Shrader 2007).

This study showed that the variety of management interventions used within both populations had little to no effect on the internal family group dynamics nor on the social population breeding group associations. Other studies have indicated that family groups amalgamate together during human interventions [e.g. response to female immobilisation (Burke 2005), poaching (Andersen and Eltringham 1997) or catastrophic fire (Woolley et al. 2008b)]. This indicates that socially-complex species might respond differently to human-induced stress, which could be due to various reasons such as the density of the population, the frequency of interventions or the intensity of interventions. It is important to use the correct range of indices as behavioural assays to determine if there is an impact on the population as a result of the intervention. Behavioural assays such as group size and distance between herds, may not always be the best indexes to use (this manuscript, Druce et al. 2006a, Druce et al. under review), but spatial and movement assays (Druce et al. 2006b, Druce et al. 2008, Druce et al. under review, Vanak et al. 2010) might be more appropriate indexes to detect a response. A more sensitive assay which could be used to measure the response to human interventions is physiological hormonal analysis (as in Burke et al. 2008, Woolley et al. 2008b). The behavioural and physiological impact assessment typically emphasizes immediate response to human activity, but the biological relevance is rarely known (Bejder et al. 2006). Therefore an understanding and knowledge of these species' social behaviour over time is essential, so that a response is not only quantified with a snap shot analysis and with a limited array of assays. However, social behaviour is only an indicator of the risk of management interventions and not a measure of its impact.

This study investigate the effects of a variety of management options, however not all options were undertaken and monitored. A further management option in Munyawana, where one of the concerns was elephant impact on the sand forest, would be to exclude elephants from the sand forest. This has now been undertaken by placing a single electric stand around certain points of the forest in order to prevent elephants from entering and to reduce any further impact on this limited habitat type. Analysis of the effect of this management action on the elephant populations' spatial and feeding behaviour, along with a measure of impact that large herbivores, such as elephant, had on the sand forest ecosystem was beyond the scope of this project but could be determined in future studies.

The rapidly increasing elephant populations within enclosed conservation areas, especially within South Africa, remains a major ecological and management concern (Slotow et al. 2005, Whyte et al. 1998). There are colossal debates, with elephants still regarded as an endangered species on the CITES list, yet many conservation areas within Southern Africa are regarded as overpopulated and at risk of destructive impact and over-utilization by elephants (Garai et al. 2004, Herremans 1995, Slotow et al. 2005). Elephants arouse major controversial concerns such as the perceived impact they have on the ecosystem and biodiversity, sustainable management, management interventions and the effect of management actions on their welfare and society. This study has indicated the importance and practicality of elephant conservation in enclosed areas by adaptive management. With such a complex, long-lived creature, management is essential to ensure the balance in the enclosed ecosystem. Stochastic events naturally control the population growth rate, size and structure, while eliminating the population's old, sickly, weak and young (Owen-Smith et al. 2005, Foley et al. 2008, Woolley et al. 2008a). Where management either control or prevent the occurrence of normal natural stochastic events, eruptive populations arise, especially within small, enclosed conservation areas (Mackey et al. 2006). Management interventions (like immunocontraception, selective hunting and culling) can be effectively used as a tool to simulate natural stochastic events (such as drought and predation) within these enclosed ecosystems.

This study is a benchmark case study for elephant managers of small, enclosed reserves, because of the variety of management interventions that were implemented within the same elephant populations in these two reserves. This ensured that the effects of all the various management interventions on these elephant populations could be compared and outcomes measured. However, one cannot exclude the fact that various elephant populations may respond slightly differently to the various management interventions. All management approaches have different levels of interference and behavioural effects, but the final decision of which options to use should be based on the management objectives of the particular conservation area. Elephant management can be flexible as there are a variety of management options available to managers of small, enclosed reserves. These should be adaptable with continuous monitoring and assessment of outcomes. Managers can learn from the actions and adapt strategically to achieve optimal management goals. Elephant management is essential to ensure the conservation and welfare of small, enclosed elephant populations, as well as to ensure the conservation of other aspects of biodiversity within these areas. Therefore elephant management is a small, but integral part of the bigger African conservation systems management, but mismanagement can have repercussions on a global biodiversity scale. Managers need to be adaptive in their way of thinking and holistic in the way they manage in order to conserve biodiversity and not only a single species but to ensure harmonious co-existence within the natural environment.

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