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Original research article

The impact of male contraception on dominance hierarchy and herd association patterns of African elephants (*Loxodonta africana*) in a fenced game reserve

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HIGHLIGHTS

- We investigate dominance hierarchies and association patterns in fenced reserve.
- All males are treated with a contraceptive: vasectomies or a GnRH suppressant.
- The treatments may have indirect effects on the elephant population dynamics.
- The rank order of the dominance hierarchy was affected by GnRH suppressants.
- The males are spending atypically large amounts of time with the female herds

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ABSTRACT

Overpopulation of African elephants (*Loxodonta africana*) in fenced reserves in South Africa is becoming increasingly problematic to wildlife managers. With growing opposition to culling and the high cost of translocation, alternative management strategies focusing on male elephants are being investigated. In this study, hormonal treatment via Gonadotropin Releasing Hormone (GnRH) suppression, and surgical treatment via vasectomy were trialled. Focusing on behavioural responses, we tested the male dominance hierarchy for transitivity, and examined the rank order of individuals in relation to age and contraceptive treatment received. Additionally, we studied association patterns between males within the male population and with the female herds.

Findings suggest that the treatment of one individual with GnRH suppressant is affecting the rank order of the dominance hierarchy, though it is still transitive, yet fluid (Landau's linearity index $h = 0.7$), as expected in a normal elephant population. Between males, association patterns were found to be weak. However, some males had relatively strong associations with the female herds, with association indices between 0.25 and 0.41. This suggests that the reduction on births is resulting in the males spending atypically large amounts of time with the female herds. The future conservation implications of this population control mechanism are discussed.

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1. Introduction

Population numbers of African elephant *(Loxodonta africana)* have increased in southern Africa since the ban on ivory hunting was imposed in 1989 by the Convention of International Trade in Endangered Species (Armbruster and Lande, 1993). Today, most of southern African wildlife is confined to a mosaic of small fenced reserves inhibiting migration and dispersal (Caughley, 1976). As a consequence, the combination of confinement, lack of natural and human predators and high reproductive success has resulted in elephant numbers reaching and surpassing the carrying capacities of many reserves (van Aarde and Jackson, 2006). This has led to local overpopulation (van Aarde and Jackson, 2006) and the attendant problems of elevated pressure on natural resources, namely vegetation and water. Overpopulation effects in small reserves are becoming increasingly evident, as high elephant population densities can result in a detrimental impact on the habitat and to other animals reliant on the same vegetation as the elephants (Landman et al., 2008).

To address these increases in elephant numbers, culling and translocations have increasingly become the principal means of controlling elephant numbers. In the Kruger National Park for example, 7% of the elephant population was being culled annually (Whyte et al., 1998). However, more recently these culling practises have attracted ethical opposition (van Aarde et al., 1999), particularly when the procedure was demonstrated to have a profound effect on remaining individuals in the population (van Aarde and Jackson, 2006). As a consequence there has been increasing pressure to explore alternative conservation management techniques, which can potentially reduce elephant numbers and their associated impacts in a non-destructive way.

Contracepting wild animals as a means to control both their population numbers and the impacts of behaviour have been the subject of considerable debate in wildlife management. For example, Asa et al. (2005) and Kirkpatrick and Frank (2005) outline the basic considerations to contemplate when choosing the method of contraception to employ, in relation to both the species involved and the problem in need of address. More specifically, several authors have considered the role of contraception in managing the negative impacts of predatory species (Bromley and Gese, 2001; Miller et al., 2013; Slotow and Hunter, 2009) whilst others have addressed the potential to reduce the numbers of free-ranging mustangs (Asa, 1999; Garrott and Sinoff, 1992; Garrot and Oli, 2013; Janet et al., 2009; NRC, 2013), white-tailed deer (McShea et al., 1997), (Rudolph et al., 2000) and North American elk (Conner et al., 2007; Heilmann et al., 1998).

To date contraception methods have largely tended to focus on females. This is because previous research into male-based wildlife fertility control in other highly social animals was drawn into question for several reasons. First, although GNRH vaccines have been shown to suppress testicular function (Janet et al., 2009), their use is contraindicated, as the testosterone mediated behaviours necessary for keeping breeding bands together is also suppressed (Kirkpatrick et al., 2011). Second, a problem with targeting males, is that if it is not a harem-based social structure, every male in the population should be treated—often not economically or practically possible (Kirkpatrick et al., 2011). Thirdly, the removal of functioning males from a breeding population may have far more serious genetic consequences than treating the females (Garrott and Sinoff, 1992; Milner-Gulland et al., 2003).

Contraception is however emerging as a viable and relatively cost-effective means of controlling elephants (Bertschinger et al., 2004; Delsink et al., 2006). In female elephants, contraceptives have been successful in delaying the age of first reproduction and lengthening the inter-calving period and have been found to have minimal impact on behaviour and social dynamics (Delsink et al., 2006; Whyte, 2001). However, treating male elephants rather than female elephants may be more efficient as fewer bulls reach breeding age; it is thought that only 39% of bulls reach the ages where they regularly enter musth, as opposed to 82% of females reaching reproductive age (Moss, 2001). One immunocontraceptive which has been used on wild male elephants is a Gonadotropin Releasing Hormone (GnRH) vaccine which inhibits the release of testosterone. The suppression of this hormone prevents the bull from entering musth, a period of heightened sexual activity, and therefore has a direct effect on the animal's overall and sexual behaviour (Bertschinger et al., 2004).

Laparoscopic vasectomies are currently being trialled on African elephant bulls. Whilst vasectomies are not reversible, because the testes are not removed in the procedure, the individual should still experience musth, undertake copulation, and maintain social status (Bertschinger et al., 2004). Vasectomies therefore provide a control mechanism which theoretically causes minimum disruption to both herd and individual behaviours. If all sexually mature bulls are vasectomised in a population, the herd birth rate should reach zero within 23 months, given that the gestation period in African elephants is 22 months and that males may be able to carry viable sperm for a short period of time after the procedures.

In African elephant, the male dominance hierarchy is transitive, yet fluid, because individuals in musth increase in dominance (Hollister-Smith et al., 2007). However, it should also be noted that male dominance in elephants is also strongly related to size and consequently age (Hollister-Smith et al., 2007). Elephant bulls grow and develop their weaponry (overall body mass and tusks) (Hollister-Smith et al., 2007) continuously throughout their life (Poole, 1989b). Size and age therefore reflect fighting ability (Hollister-Smith et al., 2007). As a consequence it is likely that the largest and eldest bull will be dominant, because that individual will experience the longest and most regular bouts of musth. Musth does not co-occur within a population (Poole, 1989a) and it has been suggested that the reason young individuals do not experience musth is that the presence of older individuals suppresses it (Slotow et al., 2000), which may explain why adolescent and young adults are often found in close association with older bulls (Evans and Harris, 2008). We can therefore conclude that musth and age are important factors in the establishment of dominance in male elephant society.

In order to determine whether male contraceptives affect population dynamics and individual behaviour, a population confined to a small reserve in South Africa was studied. Within this population, all sexually mature bulls have either been

Table 1
Vasectomised bulls associated with the A + B family herd.

Individual	Abbreviation	Age	Vasectomy date	Other contraceptive treatment
Ingani	IN	43	N/A	GnRH-IMPROVAC
Shayisa	SH	21	31-07-2008	N/A
Kohlewe	KO	16	29-07-2008	N/A
Lucky	LU	16	01-08-2008	N/A
Khumbula	KH	15	29-07-2008	N/A
Ntini	NT	15	28-07-2008	N/A
Mgangane	MG	13	30-07-2008	N/A
OJVM 1		12	N/A	N/A
OJVM 2		10	N/A	N/A
OJVM 3		9	N/A	N/A

given vasectomies or treated with a GnRH suppressant. To date the social effects of such treatments are largely unexplored, therefore in this study we look at the male dominance hierarchy to determine whether it reflects the transitive relationship that would be expected from an untreated elephant population. Additionally, the association patterns of 10 bulls ranging from 11–35 years old were investigated. Also, the association pattern of male individuals with females and other bulls were also examined to explore whether the patterns of association are as expected, or whether the bulls are spending unusual amounts of time in the presence of females.

2. Methods

2.1. Study site

The research was conducted in Pongola Game reserve east (PGR), KwaZulu Natal, South Africa (co-ordinates: $27°23'25''S31°54'37''E$); established in 1993 and covering an area of approximately 73.7 km^2. The climate in this area is hot and dry, with an annual average rainfall of 400–600 mm (Shannon et al., 2008). There is a wet season from October to March with the average rainfall for July 12 mm and temperature 26°. The dry season April to August has temperatures averaging around 17° and rainfall 110 mm in the wettest month December. (http://en.climate-data.org/location/189671/ on 21/05/14.)

2.2. Pongola's elephant population

In 1997 two family groups (A + B herd), consisting of a total of 17 individuals, were translocated from Kruger National Park to PGR. Throughout 1998, four bulls were also introduced to the park, with another three following in 2001. In 2000 a group of five young orphans, four females and one male, broke into the park from a neighbouring reserve. Today, the two family groups introduced in 1997 often form one large female herd. The orphans have remained separated from the other elephants, occupying different areas of the reserve (Shannon et al., 2006).

2.3. Study animals

At the time of the study (February 2011–July 2012) the A + B herd consisted of approximately 56 individuals and the C (orphan) herd, 17 individuals. The male population was made up of seven sexually mature bulls, all undergoing a form of contraception, and three adolescent bulls approaching sexual maturity (Table 1). The largest and eldest male, Ingani (IN), is treated with GnRH suppressant (as he was deemed at risk from any invasive operation due to his age). From November 2008 to 2011 IN received 3 mm of IMPROVAC® every eight months. In February 2011 he was observed in musth (pers. obvs. H. Zitzer), consequently his dosage was deemed to be too low and was increased to 6 mm of IMPROVAC®, administered every five months. Six young adult males were given "in-field" vasectomies. Three adolescent bulls were monitored for sexual behaviour changes as they were being considered as vasectomy candidates. All females in the population were left untreated.

2.4. Data collection

All bulls, excluding the four youngest adolescent bulls, were radio-collared at the time of the vasectomy procedures and were located using telemetry. Over 18 months, behavioural data were collected daily in daylight hours when elephants were visible. All data were collected by the field scientists responsible for the project. Positional data was collected using 30 min scans (Altmann, 1974). Once one or more individuals were successfully identified a scan was initiated. Parameters recorded during the scan were the geographic position, the total number of individuals visible, and the identity of any bulls and herds present. These scans were repeated at 30 min intervals for as long as the individuals being observed were visible.

Focal samples were conducted on the target individuals, comprising all vasectomised bulls, the only adult bull and the three vasectomy candidates to collect behavioural data. The focal samples took place in the 30 min intervals between the scans and lasted a total of 15 min. During this time all behaviours and interactions are recorded as per Altman (1974; Table 2).

Table 2
Ethogram describing behaviours categorised as dominance or aggressive for classification in the field.

Aggressive behaviour		
Threat	TH	Elephant looks directly at another elephant with head held high and ears lifted. Elephant may also shake the head abruptly causing ears to flap sharply or shake the trunk in the direction of the other elephant. The elephant may also swing their head or body round abruptly to face another individual. Rapid steps or running at another individual whilst vocalising, lifting or flapping ears is classed as a 'mock charge', which also counts as a threat.
Charge	CH	Elephant rushes towards an adversary—generally silent with head down and ears flat against the body, stopping just short of the target, forward trunk swing may follow and kicking dust. This behavioural category can include male–male chasing in which one bull follows a retreating bull as a fast walk or run.
Contact Charge	CC	Elephant rushing towards an adversary with ears spread, head raised or lowered and the charge continues until contact with the adversary is made The trunk may be curled in so that the tusks make first contact. Usually silent.
Dominance behaviour		
Non-physical Displacement	NPD	Elephant displaces another just by approaching (without contact).
Physical Displacement	PD	Elephant pushes or shoves another out of their position, and then moves in to replace them.
Trunk over body	TB	Elephant places the trunk along the back of a partner, or their head. This is typical courtship behaviour from male–female but is also a dominance display between males.
Tusk Interlocking	TI	Two elephants face each other and interlock trunks or tusks. Can escalate into pushing against each other.
Submissive Display	SD	Elephant actively shows submission by presenting their rear end to the partner and/or walking backward towards another elephant.
Chase	CS	Elephant male gives chase to signify his dominance status above the recipient: follows another bull at fast walk or run to. Behaviour is in almost all cases dominance related and in the presence of group of females/herd. The chase may lead to a dominance interaction.

The outcome of agonistic behaviour was determined by identifying the actor and recipient of the behaviour. The first individual to demonstrate submissive behaviour such as a NPD, PD or SD (Table 2) is identified as the 'loser' while the other is the 'winner'. Overall a total of 2288 scans and 1412 focal samples were collected in this study spanning 18 months.

Scan data were subsequently analysed to determine the association patterns in the population, while the focal data was used to analyse the male dominance hierarchy.

3. Data analysis

3.0.1. Dominance

The male dominance hierarchy was constructed using the focal data collected. From this, dominance interactions were extracted and incorporated into a dominance matrix. Landau's linearity index (h) (1951) was used to determine whether the hierarchy was transitive applying the following formula:

$$h = \left(\frac{12}{n^2 - n}\right) \sum_{a=1}^{n} \left[v - \frac{(n-1)}{2} \right]^2$$

$n =$ the number of individuals, $a = 1$ where an individual has dominated another and $v =$ number of individuals dominated by individual a.

An additional matrix, scoring 1 where an individual has dominated another, or 0 where the individual was dominated or where no interaction was observed, was also employed. Where the relationship could not be established, both individuals were scored 0.5. Once the additional matrix was constructed, the strength of the hierarchies' linearity can be determined using Appleby's (1983) table for the probability of linearity—the closer the result is to 1 the stronger the linearity of the hierarchy is (de Vries, 1995).

3.0.2. Dominance index

David's score (David, 1988) was calculated for each individual in the population to determine the rank order of the males in the population using the formula:

$$DS_i = w_1 + w_2 - l_1 - l_2$$

where
w_1 = the sum of i's P_{ij} values
w_2 = the sum of w_1 values weighted with the corresponding P_{ij} values of the other individuals i interacted with
l_1 = the sum of i's P_{ji} values
l_2 = the sum of l_1 values weighted with the corresponding P_{ji} values of the other individuals i interacted with P_{ij} = the proportion of wins by i over
jP_{ji} = the proportion of losses by i in interactions with j; $P_{ji=}1 - P_{ij}$.
The individual with the highest David's score was the most dominant in the population.
To calculate the steepness of the dominance hierarchy, the David's scores obtained were normalised (de Vries et al., 2006) using:

$$NDS = DS + (n(n-1)/2)/n$$

where: n = number of individuals.
The normalised David's scores (NDS) were then represented in a least-squares linear regression where the steepness is the slope (x) of the fitted line (de Vries et al., 2006).

3.0.3. Association patterns

The patterns of association between the bulls and females as aggregates were investigated using an association index (I) (Clutton-brock et al., 1982):

$$I = N_{ab}/(N_a + N_b + N_{ab})$$

where:
N_{ab} = number of occasions where a and b are seen together
N_a = number of occasions where a is without b
N_b = number of occasions where b is without a.
The closer the result is to 1, the stronger the association between groups or individuals is.
Subsequent to this analysis, the association patterns between individual bulls and the two distinct herds were analysed using the association index. In addition, any association patterns within the male population were also analysed.

4. Results

4.1. Dominance

4.1.1. Landau's linearity
Landau's formula to test for linearity, revealed that $h = 0.7$, confirming that there was a degree of linearity in the male dominance hierarchy. It is not however a strongly transitive dominance hierarchy, as $h < 0.9$ (Appleby (1983) (in de Vries, 1995)).

4.1.2. David's score
The Normalised David's (NDS) score was used to produce an ordinal rank order for the individuals being studied (David, 1988). Additionally, a least-squares linear regression was performed in order to determine the steepness of the hierarchy (de Vries et al., 2006). A total of 326 dominance interactions between adult bulls were considered in the analysis.
The NDS obtained revealed that although there was a linear rank order (Fig. 1), the eldest and largest bull (IN) was not the most dominant, instead the second eldest was most dominant (SH) followed by IN.
The gradient of the hierarchy is 0.79 (Fig. 1). This result aligns itself with that found from Landau's linearity index. The hierarchy is transitive; in this case the NDS provides information on individuals' positions in the hierarchy and the distance in dominance between them. There was a steeper decline in dominance between the two eldest individuals and the six younger bulls. IN and SH have very similar DS and NDS suggesting that they were very closely ranked in the hierarchy. LU and AS were also closely matched in dominance rank.

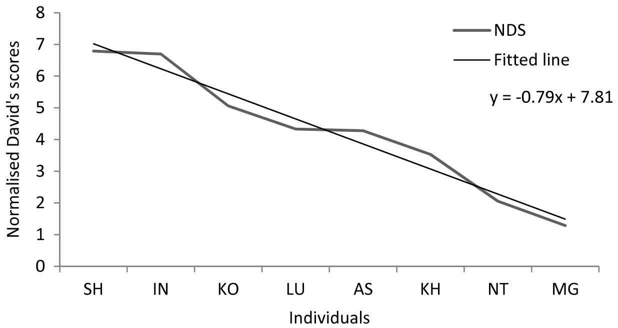

Fig. 1. Hierarchy steepness based on normalised David's scores (NDS).

Table 3
Association indices for the bulls with females, A + B herds and the Orphan herd.

	Females	A + B	Orphans
IN	0.28	0.30	0.06
SH	0.32	0.32	0.10
KH	0.35	0.37	0.07
KO	0.33	0.36	0.06
LU	0.15	0.07	0.25
AS	0.23	0.22	0.11
NT	0.40	0.41	0.10
MG	0.39	0.37	0.14

Table 4
Association indices for the males.

Individual	IN	SH	KH	KO	LU	AS	NT
SH	0.24						
KH	0.03	0.13					
KO	0.31	0.03	0.23				
LU	0.10	0.06	0.04	0.04			
AS	0.09	0.26	0.61	0.24	0.10		
NT	0.30	0.29	0.12	0.11	0.05	0.27	
MG	0.31	0.11	0.03	0.24	0.09	0.32	0.10

4.2. Association patterns

4.2.1. Bulls with females

The association patterns of bulls with females showed that NT had the strongest association $I = 0.40$ (Table 2). IN, LU and AS had the weakest association with females, with I ranging between 0.15 and 0.28. NT had the strongest association with the A + B herd ($I = 0.41$) but a weak association with the orphan herd. KH, KO and MG had very similar indices with the A + B herd, while IN, LU and AS had the weakest association with the A + B herd. All bulls showed a weak association with the orphan herd, with LU demonstrating the strongest association with $I = 0.25$ (Table 3).

A + B has an association index of 0.8 while the orphan herd had an index of 0.47 with bulls as a whole.

4.2.2. Bulls with other bulls

The strongest association was between AS and KH ($I = 0.61$). Weaker, yet still notable associations, include IN and KO (0.31); IN and MG (0.31) and AS and MG (0.32) (Table 4).

NT had the strongest associations with the other bulls overall, while LU showed the weakest. SH and IN, the two eldest bulls had a relatively weak association as we would expect (Table 4).

5. Discussion

Most studies to date have focused on understanding the behaviour and social structures of the female family herds. Although some have concentrated on male social behaviour and structure Poole (1987), Poole (1989b); Wittenmeyer et al. (2005), Hollister-Smith et al. (2007), Evans and Harris (2008), none assess male dominance hierarchy and the patterns of association with female groups and other bulls in a population where male individuals have been treated with contraceptives. This study is therefore unique in that it observes a population in which all adult bulls are treated with some form of contraceptive.

The key focus of the research was to determine whether the male dominance hierarchy is constructed as would be predicted post contraception. In order to assess this, the steepness of the hierarchy was calculated to determine the distance in between individuals, thus providing a measure of degree of dominance between the males. The resulting dominance hierarchy was found to be linear, but not strongly so (see Fig. 1), indicating that the individual bulls are comparatively well matched in their herd status. Interestingly our results indicate that SH, the second eldest bull was the most dominant, as compared to the expected dominance of IN (as a consequence of his size and age).

The dominance rank order score revealed that SH, the second oldest bull, is more dominant than IN (the oldest). From the dominance interaction behaviour collected over 18 months it is evident that the total number of dyadic interactions that IN was involved in was low, with only 18 as opposed to 55 for SH. This may explain his position in the hierarchy below SH, even though IN lost no interactions, whilst SH did. This is an interesting finding in that although IN was showing decreased rates of interaction with other bulls, he was evidently still physically capable of dealing with challenges from all other herd members when engaged. IN and SH had an association index of 0.24, which in comparison with other results found was high. This suggests that either SH is seeking out IN, possibly in order to gain knowledge, or that IN spends time with SH in order to suppress his musth (Evans and Harris, 2008). IN was found to have stronger associations with two younger bulls, KO and NT aged 17 and 15 respectively, who have both been observed in musth (pers. obvs. H. Zitzer). Again, these could be indications that the younger bulls have located IN in order to utilise him as an educator, or that IN seeks them out in order to suppress the occurrence of musth, thus securing paternity of any offspring.

The gradient of the hierarchy curve (0.79) indicates that the distance in dominance between the most dominant and least dominant bull is significant. Conversely, there was limited distance between the two eldest bulls (IN and SH) in the dominance rank order (Fig. 1). This could suggest that IN is the most dominant bull as would be expected when considering the demography of the male population. His position as 'second' may be a due to a lower number of interactions with the younger bulls as a result of reduced testosterone level and therefore loss of interest in asserting his position. Additionally the marked difference in size and age between him and SH means that he is not required to physically defend his position in the hierarchy.

Other individuals that were found to be very closely ranked were AS and LU (Fig. 1). They are both of the same age and of a similar size (Table 1), thus supporting the supposition that dominance is a consequence of age and physical characteristics. The data indicates that the relationship between AS and KH was the closest, as they had the highest number of dominance interactions and the strongest association score. This corroborates the suggestion that young bulls seek individuals of a similar age upon leaving the natal herd in order to practise sparring (Evans and Harris, 2008). NT, who is the same age as both AS and KH, is ranked considerably lower than them and is closer to MG who is 13 years old. This may be explained by his strong association with the A + B herd—his natal herd. He had the strongest association with the females in the population and the A + B herd in particular ($I = 0.41$; see Table 3). LU has the weakest association with the females, although he has the strongest association of all the bulls with the orphan herd.

African elephant bulls begin to leave their natal herd when they reach sexual maturity (Poole, 1989b). They then temporarily associate with other female family groups, form a bachelor group, or roam independently (Poole, 1987). If there are females in oestrus in the vicinity, bulls old and young are likely to follow the distribution pattern of the receptive females (Wittenmeyer et al., 2005). The birth rate at PGR will have slowed since the implementation of contraception in 2008. This reduction in pregnancies may have resulted in increased rates of oestrus (Bertschinger et al., 2004) within the PGR population. As adult male elephants seek out females when they are in oestrus (Wittenmeyer et al., 2005), the A + B herd, which comprises approximately 65 individuals, is likely to have at least one female in oestrus at any one time.

The demographic structure of the male population at PGR is of particular interest, with one large bull, IN who is 43 years old, the next oldest bull, SH, being 22 years younger, and the other bulls aged between 16 and 13 (Table 1). This demographic should render the oldest bull (IN) the "educator" of the younger bulls Slotow and van Dyk (2001). However, the dominance hierarchy results indicate that he is not the dominant male and therefore may have lost that role, potentially introducing long-term unrest to the herd as a consequence of aberrant behaviour among the sub-adult bulls. This research shows that since the implementation of contraception at PGR, there have been several births, indicating the possibility that the sub-adult males are fathering calves. This is of particular concern as these individuals would be unlikely to assume mating rights under normal conditions due to their inferior body and tusk size and therefore raises questions as to the long-term genetic fitness of the herd over time. Similar phenomena have been reported in studies of wild mustang (Asa, 1999) and North American elk (Heilmann et al., 1998) and in this study raises the possibility of either a much wider ranging application of contraception across males within the herd (if we are to target males to achieve zero productivity) or a cessation of the method overall, as has been the case for other species in the past (Garrott and Sinoff, 1992).

Dominance ranks depend on size and age in male elephants, however musth also affects dominance (Poole, 1989b; Hollister-Smith et al., 2007). Therefore the occurrence of individuals in musth in a population will lead to the hierarchy being to some extent changeable. Being the eldest and largest, IN should be dominant for the majority of the time, which he clearly is not. This is likely to be a consequence of his treatment with GnRH suppressant which affects hormonal balances and, when administered in the correct dosage, prevents musth (Bertschinger et al., 2004). However, new-born elephants on the reserve suggest that the GnRH vaccine administered to IN might not working effectively, possibly due to incorrect and irregular dosing. The incorrect dosing proposition is supported in that IN has also been observed in musth on several occasions since the contraceptive treatment began (pers. obs. H. Zitzer). Despite this he may still be experiencing hormonal imbalances that in turn affect his behaviour, particularly his agonistic behaviour towards other bulls. Linked to this is the possibility that the particular GnRH vaccine employed is not working as well as expected, leading us to suggest that exploration of alternatives be undertaken.

Research on African elephant social structure and population control is largely focused on females rather than males. This study shows that the behaviour of bulls in a population is potentially influenced by population demographics and human interferences. Results obtained from this study demonstrate that behaviour in male African elephants can be severely affected by both demography and management decisions, which in this case were made to address overpopulation. The combination of the demography of the male population and the two different methods of contraceptive applied to this population demonstrate that male social structure is as complex and vulnerable to interference as the female. Further investigation into changes to male social structure on a longer term data set to fully encompass the long term effects of applying contraceptive treatments to a population may yield more conclusive results.

Due to the lack of pre-vasectomy behavioural data for this population, a comparison with an untreated population occupying a similar sized reserve would be optimal to fully quantify the effects that GnRH suppressants and vasectomies have on male elephant social structure. Further research into the occurrence of musth in young individuals and those that have been given vasectomies would elucidate the effects that contraception and the demography of the population has on behaviour. Finally, it would be interesting to investigate whether females are experiencing higher rates of oestrus due to reduced birth rates as result of the vasectomies, which not only affect their behaviour, but also influence the behaviour and ranging patterns of males (Wittenmeyer et al., 2005). Further insight into behavioural changes that take place as a result of population control management strategies is essential to ensure that any longstanding interference with free ranging animals has a minimum impact on the social structure and individual behaviour.

We conclude that male dominance and association patterns are important factors to consider when studying social relationships, particularly in species with complex structures, such as the African elephant. Gaining an understanding of social dynamics in fenced reserves will become increasingly important from a conservation management perspective, as more reserves experience elephant overpopulation over time (van Aarde and Jackson, 2006) and the resulting pressures they exert on their environment. Furthermore, this research highlights the importance of careful consideration when translocating African elephants to small private reserves. The introduced population will in effect grow to create a genetically isolated population. For this reason careful thought should go into how the demography of the population can be expected to evolve over time and how population control could be implemented before overpopulation occurs to minimise scenarios where all male individuals in a population require contraceptives in order to address severe overpopulation problems.

These changes reflected the expected nexus between a species with polygynous social structure and strong group fidelity and the large instantaneous change in population density and demography coincident with culling.

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