SAVE THE ELEPHANTS

South Africa

Report on the demographics of the bull population of the Associated Private Nature Reserves

2013

soon to become

elephants alive!

Research & Conservation

by
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(PhD)

INDEX

ACKNOWLEDGEMENTS

Although convention dictates for acknowledgments to be placed at the end of a body of work, I would like to thank the following people first and foremost for their continued support and assistance over many years. Any long term identification study necessitates the team work required with the continual collection of thousands of photographs and the subsequent processing thereof. The transcription of this information into various models to obtain population estimates, again requires the involvement of a few dedicated experts that understand the long hours involved in preparing input files. During each of these phases I have had the privilege of working side by side with various individuals to whom I am most grateful.

Firstly, I would like to thank Barry Paul for the many hours that he has spent not only assisting with the entering of elephant identification photographs over the past two years and the training of people to use to the pattern recognition software which is still a work in progress, but also for the time and dedication he took in programming output files for the models. The time you have devoted to this cause and often under difficult circumstances whilst being immersed in your own profession or even in hospital, has not gone unnoticed and unappreciated. I hope to spend many satisfying hours in the field with you where we not only find and photograph numerous unknown individual elephants, but also end the day with the rewarding experience of near instant matching of a particular individual to an automated identification system. Thank you also for all the encouragement and moral support throughout this project.

I would like to thank Dr. Lex Hiby for his patience and guidance in answering all our questions regarding the use and implementation of his pattern recognition software. We are not there yet, but the end is in sight and the goals have been set. Dr. Pierre Pistorious and his PhD candidate, Rabi'a Ryklief thank you for all the expert advice regarding the use of the MARK software for the survival analyses and population estimates respectively. It has been a pleasure working with the both of you and I know there are numerous hours that still lie ahead of us but I look forward to the road ahead.

Then I would like to make special mention of a handful of friends and family members who have spent hours assisting with the collecting and processing of elephant photos. These include Amy Clark, Angela Segal, Anne Anderson, Cathy Greyling, Hannah Malin, Jennifer Blondeau, Sarah Bergs and Shirley Michael. Thank you to my dearest Mother who put me on this journey in the first place with the collection of the first elephant identification drawing way back in 1996! To the rest of you mentioned above that joined the addiction over the past two years, I notice and fully appreciate the hours of dedication that you have put in at one point or another.

I would also like to thank the following people for assisting with the collection of elephant identification photographs and who were either directly involved in the project at some point in time or who represent managers, landowners or interested parties within the Associated Private

Nature Reserves. In particular, I would like to thank Transfrontier Africa and all their volunteers who have submitted photographs taken in Balule Private Nature Reserve under Craig Spencer's guidance since 2008. Each good elephant identification photograph represents a brick contributing towards the body of knowledge that will allow us to improve our understanding of their movements and social relations. Thank you all for supplying the bricks while we keep building the house: Adam Edge; Adrienne Eacrett; Alison Foster; Alister Wood; Andrea Webster; Andreas Liebenberg; Andrew De Luca; Angela Segal; Anique Willems; Amy Clark; Andre and Stefanie Ganswindt; Anne Anderson; Alexander Munro; Axel Moberg; Bill Sonnenberg; Brendon Shmikl; Brian & Claire Makare; Cassie and Kate Carstens; Carl van der Berg; Cathy Greyling; Ceasar Maseola; Chad Cocking; Charlie Irish; Chris Hall; Chris Galliers; Christiane Knechtel; Christine McCagh; Clive Smith; Craig Fox; Colin Addis; Cornelius van der Waal; Craig Spencer; Colin Rowles; Craig and Melissa Ferguson; Dale Jackson; Dartmouth College students; Dave Jackman; Dean Griffiths; Dennis Rutter; Don Scott; Doug Schaefer; Ed and Sally Mayer; Edwin Pierce; Emeric Blondeau; Francois van der Merwe, Frankie Berndt; Gabrielle Simmons; Georgette Lagendijk; George Piel; Glenn and Craig Catton; Gordon Jones; Gustav Roux; Hannes Zowitsky; Hannah Malin; Hettie Ueckermann; Ian Peltzer; Ian and Tersia Sharp; Ian Whyte; Ivo Lazic; Janine Scorer; Jennifer Blondeau; Jody Cole; Joe Brady; Johan Marias; John and Keeley Clack; John Braithwaite; John Griffin; John John Nicholson; Josh Hibbett; Joubert de Lange; Judith Foster; Jurgens Wilson; Keith Jenkins; Kelly Durham; Kerry-Lee Dyer; Kevin Blatherwick; Kgoala Shai; Laurent Scharapan; Lauren Wilson; Lars Sund; Lenie Oosthiuzan; Les Penfold; Lia Edkins; Lisa Baardsen; Lonnie Strickland; Marc Riley-Hawkins; Mark Griffiths; Mark Freeman; Marius Fuls; Martin Stone; Matthew and Tiffany Steyn; Melody Bates; Mette Rossaak; Naomi Martin; Natalie Jean; Neil and Morag Hulett; Nelda Villines; Neil Malan; Mwana Bermudes; Nikky Parkin; Patrick Freeman; Patrick O' Brian; Patrick O' Connor; Pamela Zweerts; Pat and Eileen Donaldson; Pat Dewil; Paul Roberts; Paul White; Paw Gosmer; Peter Anderson; Peter Smelting; Peter Thorpe; Pieter Nel; Prince Nkuna; Quintin Hagens; Rebecca Fitch; Richard Sowry; Rob Panos; Rodney Topham; Ronnie Makukule; Rob Braid; Rudi Goerke; Sarah Bergs; Shirley Michael; Sidney Rebe; Sieglinde Rode; Sinhle Matebula; Simon Evered; Stefan Bosman; Stefan Breuer; Steve and Michelle Panos; Steve Henley, Summer Shaw; Susanne Vogel; Theresa McDonald; Tim Paxton; Timothy Hancock, Tony McClellan; Trish Pontenyn; Virginia Pearson; Walter Jubber from Wilderness Safaris; Willem Nortier; Willie Sonnenberg; Yolanda Pretorious; Yuval Erlich.

To all our financial sponsors that have kept us afloat, a very special word of appreciation. Numerous private donors have contributed towards the collaring operations. Overall, we would like to thank the U.S. Fish and Wildlife Services and the Wildlife and Environmental Society of South Africa for their long-term support.

Last but not least, I would like to thank my parents and Marlene McCay for their unfailing support and encouragement. You have carried me with your kind words and caring gestures in more ways than you will ever know.

EXECUTIVE SUMMARY

According to contractual agreements, Save the Elephants–South Africa has been asked to provide the Management Committee of the Associated Private Nature Reserves (APNR) with the numbers of bulls within specific age categories to enable management to decide on off-take figures for the upcoming hunting season. This information was gathered from a long-term elephant identification study which officially started in the APNR in 2003. Drawings were made of each individual elephant based on the photographs collected within the APNR. For the study period 2003 to 2011, a total of 83 212 photographs of individual elephants, were collected by registered researchers and processed to produce identification drawings for 1125 and 353 individually identified bulls and cows respectively. These identikits were collected during 3186 encounters with multiple or lone elephants which transcribed to 6460 individual encounters with either a bull or a breeding herd as a collective unit. Various Mark-recapture models were used to obtain estimates within specific age categories and the results were compared with annual aerial census results that have been collected and collated within the APNR over the past 20 years. Analysis of GPS location data obtained from collared elephants was used to develop and choose the most suitable models for the analysis. The following results were obtained for each of the specified age groups:

Estimates of abundance using the Jolly-Seber model (estimate ± SE) for the immature, young adult, adult, prime adult and senescing age categories of elephant bulls found within the APNR.

Year	Immature	Young	Adult	Prime	Senescing	TOTAL[1]
2003	0	0	0	0	0	0
2004	0	121 ± 63	151 ± 38	124 ± 13	6[2]	406 ± 47
2005	11	60 ± 4	92 ± 10	84 ± 4	7	263 ± 11
2006	19	66 ± 4	83 ± 4	73 ± 1	9 ± 2	255 ± 7
2007	15	92 ± 6	92 ± 4	64 ± 2	6 ± 1	191 ± 8
2008	18	89 ± 5	77	48 ± 2	9 ± 2	243 ± 6
2009	10	36	15	15 ± 2	5 ± 1	85 ± 5
2010	47	54	23	16 ± 2	3	154 ± 6

[1] *The total as calculated by the model and not the sum of the respective cells*
[2] *Standard errors that round to zero are not included in the table*

The results from the models and various trends relating to census and mortality figures were used to provide Management with recommendations for consideration.

INTRODUCTION

According to contractual agreements, Save the Elephants–South Africa has been asked to provide the Management Committee of the Associated Private Nature Reserves (APNR) with the numbers of bulls within each of the following age categories by making use of the elephant identification data collected from 2003 until 2011:

- Immature <15 years
- Young 15-25
- Adult >25-35
- Prime >35-55
- Senescing >55

The data will be used to set proposed off-take numbers for the upcoming hunting season.

METHODS

Field methods

Individual identification records of sighted animals (bulls and cows) were recorded by collecting detailed photographs based on unique patterns of tears, nicks, holes and veins in the ears of all elephants encountered when searching for collared elephants on a rotational basis throughout the APNR. The method of using individual physical features of ear patterns in combination with any other feature such as scars to the body, tail hair features and tusk shapes, are well established and have been employed by various studies throughout Africa (Douglas-Hamilton 1972, Croze 1974, Jachmann 1980, Whitehouse & Hall-Martin 2000, Moss 2001, Wittemeyer 2001). Photographs were also collected of the frontal line patterns of the face from the base of the tusks to the forehead to make allowance for individual identification via pattern recognition software which is currently being developed and tested. The date, time and GPS location of each sighting was noted in addition to the group size, social context, the reaction index of the animal to the researcher as well as the reproductive status of bulls (musth or non-musth).

All bulls were categorised into various age categories using a combination of characteristics based on size, physical development, eruption of tusks, the length and circumference of the tusks and body shape and proportions (Moss 1996, Poole 1987, Henley 2012). Other than the age categories into which elephants were assigned during field observations, two experienced elephant researchers aged each of the bulls independently from the identification photographs that were collected during the first sighting occasion of an individual. The average age was taken across these assigned age categories and the age at present calculated based on when the animal was first sighted and photographed. For the purpose of this report, finer age categories were collapsed into five age groups (refer to Table 1 highlighted in yellow) with the focus being on bulls only. A record was also kept of bulls that were sighted with tusks in the region of 80lbs or more aside.

Drawings were made of each individual elephant based on the photographs collected in the field. For the study period 2003 to 2011, a total of 83 212 photographs of individual elephants, collected by registered researchers were processed to produce identification drawings for 1125 and 353 individually identified bulls and cows respectively. These identikits were collected during 3186 encounters with multiple or lone elephants which transcribed to 6460 individual encounters with either a bull or a breeding herd as a collective unit. Photographs submitted by landowners and other interested parties with the required date and time sighting information for

Table 1: Age categories for bulls and behavioural characteristics associated with each category.

Age class	Age category	Broad age class	Age category	Behavioural description
0-4	neonates, yearlings and juveniles			still nutritionally dependent on mother
5-10	sub-adults			nutritionally independent of mother but socially dependent on natal herd
11-15	sub-adults	<15	immatures	nutritionally independent of mother but socially dependent on natal herd
16-20	young adult			becoming socially independent from natal herd, socially dependent on male mentors, no musth
21-25	young adult	15-25	young adults	becoming socially independent from natal herd, socially dependent on male mentors, no musth
26-30	adult		adults	socially independent from natal herd, socially dependent on male mentors, start of musth cycles
31-35	adult	>25-35	adults	socially independent from natal herd, socially dependent on male mentors, start of musth cycles
>35	prime adult	>35-55	prime adults	socially independent from natal herd, male mentor to younger bulls, start of regular, annual musth cycles
>55	senescing adult	>55	senescing adults	Male mentor to younger bulls, musth cycles continue until body condition deteriorates

use in mark-recapture analyses, were used to add additional records of bulls with large tusks to the database even if the photographs often lacked the associated spatial data and social context of the sighting. All photos taken in the field of individual elephants were manually compared with the individual elephant drawings to find the drawing with the closest match. A potential match was then double-checked by comparing the photographs of the newly found individual with those kept in the photo library of a specific individual. Only if the library photographs confirmed a match between a library drawing and a newly photographed individual, was the encounter of a particular individual recorded as a resighting. Where field photos were collected during suitable lighting conditions and the aspect of the elephant frontal view was considered appropriate, wrinkle patterns of the face were extracted to slowly build up an individual elephant identification library using the pattern recognition software (Conservation Research Ltd.; Extract Compare V1.18, Cambridge; L. Hiby 2011). With time and the extension of the facial line-pattern library, the software was also used to call up the closest match of a newly photographed individual but final checks were still confirmed via the manual method while the software is under development.

Data analysis

Aerial census and mortality data

Results from the mark-recapture models were compared with annual, aerial census and mortality data obtained from the Kruger National Park (KNP) and the Wardens of the APNR. Where the KNP conducted census surveys within the APNR, these were used to ensure consistency in the methods used over the larger study area. A distinction was made between elephant mortalities due to anthropogenic (trophy hunting, problem animal control, euthanasia following injury, illegal poaching, snaring or death on roads or railway lines) or natural (conflict, disease, old age or unknown) causes for records obtained from the APNR. Where dead elephants could be identified from the photographs taken or submitted by the Wardens, these records were incorporated in the Immigration-Emigration log-normal estimator (IELNE) as these animals would no longer be available for resighting (McClintock & White 2010). Photographs for identification of dead elephant bulls were only available for 33% of all recorded mortalities within the APNR of which only 40% of the elephants could be identified due to the quality of the photographs available. Hence mortality records incorporated in the model are under-represented which in turn could overestimate abundance and survival estimates.

Mark-resight models for estimates of abundance

Mark-resight models provide estimates of abundance (*N*) as with Mark-recapture models but instead of capture periods, resighting periods enable encounters of marked individuals as well as sightings of unmarked individuals into the estimation. The methods used during Mark-resighting models are cost effective as the costs associated with marking and recapturing are minimised and associated with minimal interference. In the case of the elephant identification study, each identifiable feature that was recorded could be considered a ‘mark’ with each of the ear marks being permanent and individually identifiable. Although marks could change (holes near the ear edges can, for example, pull through and become a ‘nick’), all features were present in one form or another and additional marks could only be added over time (Morley & Van Aarde 2006).

Various Mark-sight models are available for estimating population size. Each model has certain assumptions associated with it's use. A general assumption applicable to all models is that the subset of the population selected for marking is representative of the entire population in terms of resighting probabilities. Furthermore, marks themselves must not affect sightability. Care was therefore taken to not only photograph elephants with characteristic ear patterns, but all elephant bulls present at a sighting and within a certain age bracket were photographed, including individuals with indistinct ear patterns. Upon careful inspection of the photographs taken in the field, unique patterns in the veins of the ears were used to distinguish these particular individuals. It should however be noted that no ear patterns were collected from any individuals younger than five years of age as their distinguishing features were thought to still appear later in life and as these individuals were also not easily sighted within breeding herds compared to the more mature bulls in older age categories.

In this study we made use of two 'marked' subsets of the population to arrive at overall population estimates which would account for emigration and immigration into the APNR. Firstly, we used the smaller subset of individuals with GPS tracking collars to provide information on movement patterns which could be incorporated or provide background information on emigration patterns of the larger sample size of individually identified elephants during model predictions. Analysis of GPS radio collared individuals clearly showed that once collared, they could move out of the study area for set periods of time, depending on their age group. Furthermore, collared elephants' movements indicated that only one out of 34 individuals that were originally collared had not returned to the APNR on an annual basis. Four out of five other individuals did not return to their capture site due to death outside of the APNR whilst one of these individuals' collars was retrieved outside of the reserve before battery failure. Hence permanent emigration from the study site appears to be minimal but models that incorporate temporary immigration and emigration are required in the analysis as geographic closure could not be assumed. Collared bulls ranged in age from 12 to 55 years, predominantly determined in the field on facial shape, tusk size and general physical appearance (Moss 1996; Poole 1987, Henley 2012). Three bulls were aged during collaring operations when the lower jaw relaxed sufficiently to enable molar measurements to be taken. Dental impressions were taken from 11 bulls based on the methods of Rasmussen et.al. (2005). We used Speedex Putty as silicone-based impression material together with Universal Activator from Coltène/Whaledent AG (Coltène, Altstsätten, Switzerland). Age estimates (accurate within ± 3 years) were made from all molar progressions as described by (Laws 1966, Sikes 1971, Jachmann 1988, Manspeizer & Delellegn 1992, Lee et. al 2011). The GPS location data of all collared elephants were plotted in ArcGIS 10.1 (ESRI 2012) and the Analysis tool used to clip data within the borders of the APNR. After grouping the collared elephants data according to the various age categories previously described, the number of locations within and outside of the APNR per individual elephant on a monthly basis was determined. Thereafter data was pooled across individuals within the same age category and the relative proportion of locations spent outside the APNR to the complete dataset for a particular age group was determined. The total proportion of time spent outside of the APNR was then equated to months and the months with the highest consecutive proportion of locations outside of the APNR which fell within defined seasonal intervals (refer to the secondary sampling occasions defined below), were used to predict when the other identified elephants within the same age bracket as the collared elephants, would be outside of the APNR. In a sequential manner, starting at the predetermined seasonal interval within the first year and ending at the ninth, each identified elephant was coded to be marked/identified but outside of the APNR. This made allowance for all identified elephants to be considered outside of the APNR at least three times over the predetermined period of highest frequency across the years but also allowed for individual movements outside of these periods albeit at a lower frequency.

Three types of models were used for this report. The original Jolly Seber (JS) model (Jolly 1965; Seber 1965) is appropriate for open populations although one assumption that will be violated with the use of this model is the incorporation of Balule Private Nature Reserve into the APNR after the removal of the fences in 2006. Hence the study area did not remain constant but increased over time which could influence population estimates. Using the software program MARK (G. White, Colorado State University; White and Burnham 1999), both the Robust Design (RD), which represents as combination of assumptions for closed population and the JS- methods (Kendall 2013), and the IELNE obtained from the use of the Immigration-Emigration Mixed Logit-Normal Marked Resighting Model appropriately also provides information on population estimates when the following is applicable (McClintock & White 2010):

- The population is not geographically closed. Although the JS and IELNE is specifically designed for use in open populations, there are certain restricted scenarios under which Robust Design models can accommodate movement in and out of the study area (Kendall et al. 1997)
- Estimates are needed for the population actually within the study area during the period of interest (APNR).
- Estimates of the super population (N^*) within the greater study area would also be of interest.
- Primary sampling sighting occasions exist which was taken to be annual events from 2003 until 2011.
- Secondary sampling sighting occasions exist within each primary sampling occasion. These periods were set at quarterly and of three months duration within each year to correspond with early dry-season (April-June), late-dry season (July-September), early wet-season (October-December) and late wet-season (January-March) movements.
- Individuals could move freely in and out of the study area under consideration (APNR) between secondary occasions of each primary interval.
- Sampling without replacement within secondary sampling sessions was upheld by pooling possible multiple sightings of an individual within this period to ensure that a single individual was only sighted once during the sampling occasion.
- Information is provided on whether or not each marked or identified individual was available for resighting within the study area for each secondary sampling occasion. Data obtained from GPS collared individuals was used for this purpose.
- All animals encounted during a sighting and which were aged but could not be identified as sufficient photos of good quality could not be taken, could still be incorporated into the model after counting the number of animals found and subsequently categorised as 'marked but unidentified' during the 36 resighting sessions defined over the study period of interest (applicable to the IELNE).
- Likewise, all animals encounted during a sighting but only briefly sighted upon arrival could be incorporated into the model outputs after been categorised as 'seen but unmarked'. These animals were ascribed to the five predefined age categories by using the same relative proportions of known aged individuals categorised as 'marked but unidentified' (applicable to the IELNE).
- Marks are preferentially individually identifiable
- New marks may be introduced at any time either during primary or secondary sampling occasions (applicable to the IELNE).

Survival analysis

Encounter-history matrices, which are required for capture-mark-recapture analyses, were constructed from the resighting data of uniquely identified elephants treating the first sighting of an elephant as the initial release. Multiple sightings during any given year were treated as a single sighting to estimate annual survival rates for each of the abovementioned age groups. Resighting data up to the year 2011 were used, which yielded 8 resighting occasions were an elephant uniquely identified in 2003, which effectively represents the first release. The software program MARK (G. White, Colorado State University; White and Burnham 1999), which is an application for the analysis of encounter-history matrices of uniquely identified individuals, was used to obtain likelihood estimates of annual survival and resighting probabilities. The software program provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model, but also under several models that appear as special cases of this model (Lebreton et al. 1992). The two fundamental parameters in these models are: Φ = the survival probability for all animals between the i^{th} and $(i + 1)^{th}$ encounter occasion (i = 1, …, k –1), and p = the resighting probability for all animals in the i^{th} encounter occasion (i = 1, ., k). The survival probability incorporates both death and permanent emigration of individuals and can therefore be referred to as apparent survival. As mentioned previously, permanent emigration from the APNR appears to occur at very low frequencies over the study period of interest. Model fit to the global model was done in program release goodness-of-fit procedure (Burnham et al. 1987) implemented in program MARK to check whether the assumptions pertaining to the model were met (see Lebreton et al. 1992). A candidate set of models with constraints on survival and resighting probability (assuming both of these to be either year specific or constant over the study period) were considered. Akaike's Information Criterion (AIC_c) was used for model selection according to the principles of parsimony (Lebreton et al. 1993; Anderson et al. 1994). Models with a $\Delta AIC \leq 2$ were considered to have substantial support from the data (Anderson and Burnham 1999).

The survival and resighting probability of bulls which were sighted with with tusks of 80lbs or more over the study period of interest, were analysed separately in view of their vulnerability to illegal poaching and unregulated trophy hunting outside of the Private Reserves and the KNP.

RESULTS AND DISCUSSION

Aerial census and mortality data

Fluctuations in population size are always more apparent in smaller areas when compared to larger study areas. Total elephant population densities were most dependent and similar to counts obtained from breeding herds of elephants. When considering the trends in the adult bull segment of the population (immature and young bull segments of the population are not discernible during annual aerial censuses whilst amongst breeding herds), there are indications of a decline in densities from 2007 onwards for both the KNP and APNR study sites. The low calf densities obtained for the APNR over the 20 year period are probably more indicative of variations in counting methods than actual numbers (Figure 1).

When comparing the relative proportions of elephants within specific group types to the total population size for the APNR and the KNP, a significant positive relationship was found between the adult bulls in the APNR and KNP (r^2=0.943, t=18.2,df=20, P<0.0001) with the same positive relationship for individuals within breeding herds across the different reserves (r^2=0.995, t=101,df=20, P<0.0001) (Figure 2 & 3). These results substantiate the connectively between the reserves since the fences were removed. The mean difference in the proportion of adult bulls within

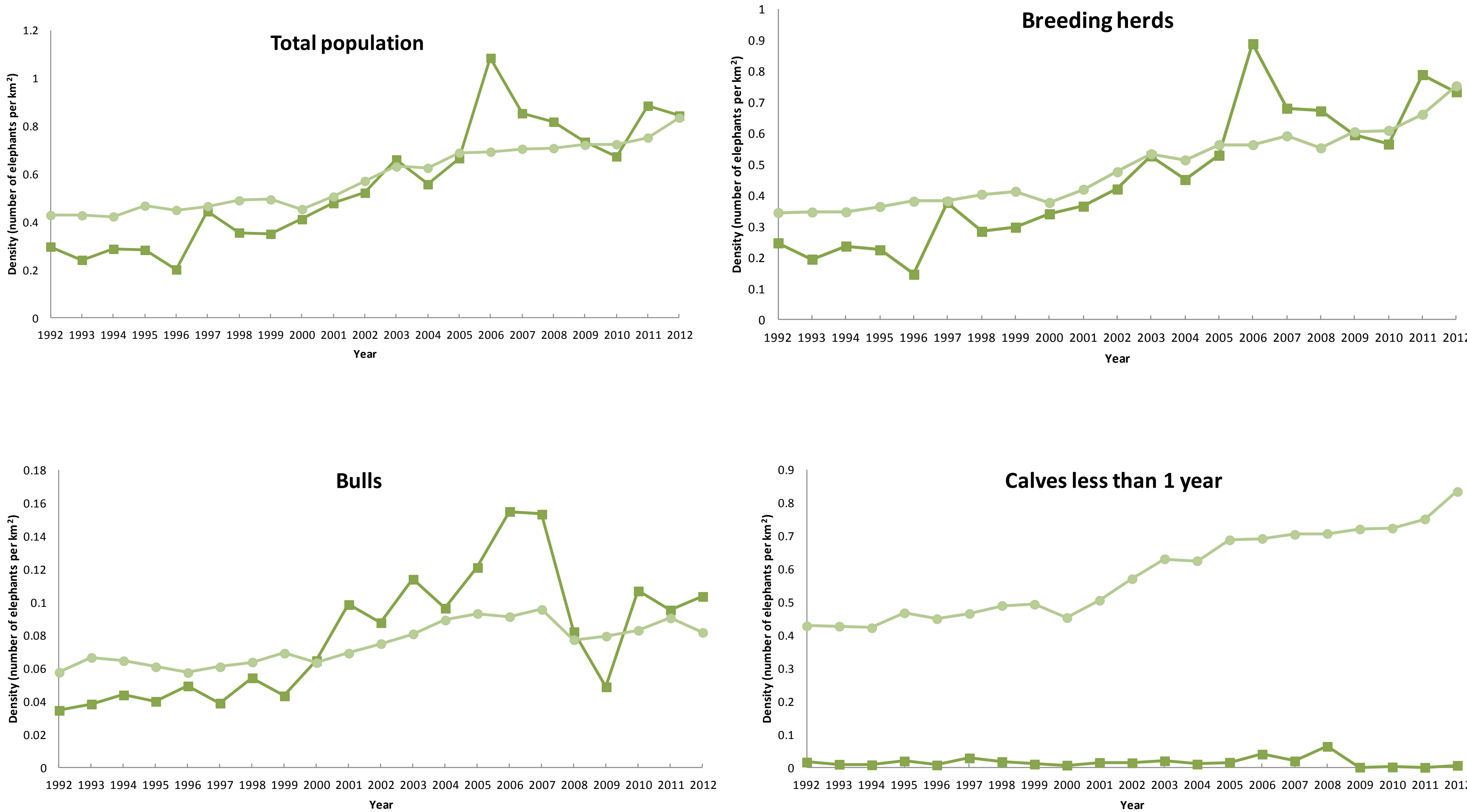

Figure 1. Trends in population densities over a twenty year period for the total elephant population in the Kruger NP (light green. closed circles) and the APNR (dark green, closed squares). The trends in the densities of different segments of the population are shown for the breeding herds, adult bulls and the calves according to the annual aerial census figures.

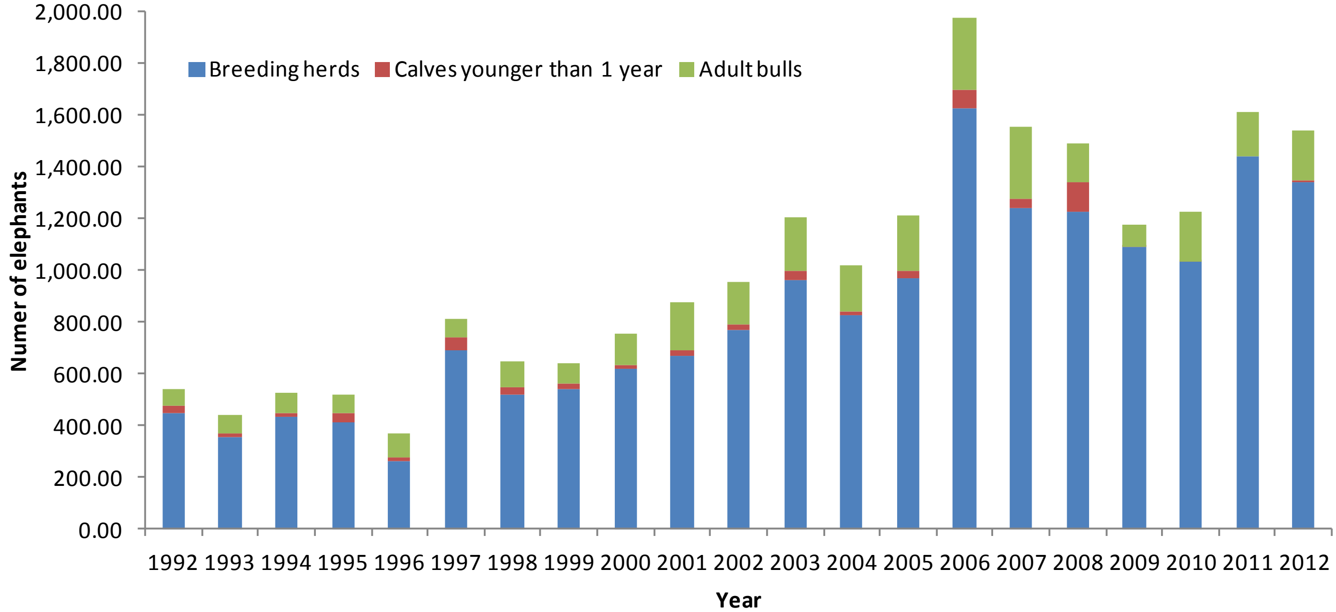

Figure 2. Relative frequencies of elephants counted in breeding herds with calves less than one year shown separately, and in adult bull groups during the annual aerial census of the APNR for the past 20 years.

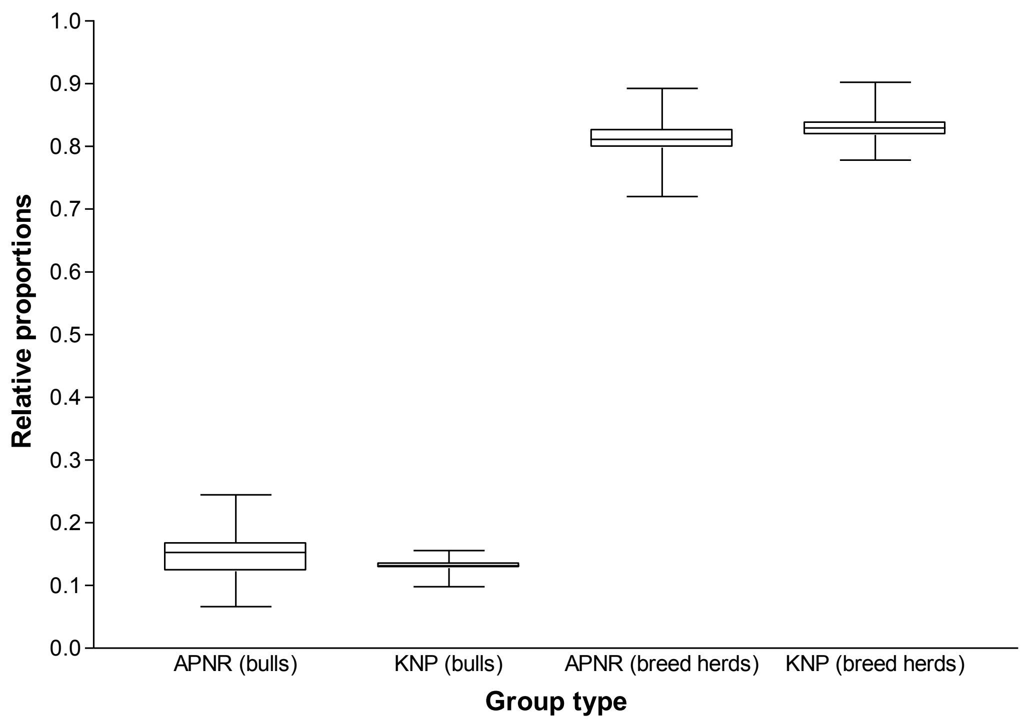

Figure 3. Box whisker plots with the box extending from the 25th percentile to the 75th percentile with a horizontal line at the median (50th percentile) while the whiskers extend from the smallest to the largest value for the relative proportion of adult bulls or breeding herd animals counted in relation to the total population number for both the APNR and the KNP.

the APNR was however significantly higher when compared to those in the KNP (Paired t test, $t=2.20$, $df=20$, $P=0.0400$) although no difference could be found when comparing the relative proportions of individuals within breeding herds to the total population size in each of the reserves. These results could indicate that either more bulls are being born within the APNR when compared to KNP or that adult bulls are immigrating into the reserve more frequently than what they are emigrating out of the APNR. Consequently, the APNR could represent a sink area for the adult bull component of the greater population which may lead to certain behavioural (immigration and emigration patterns) and/or physiological responses (increased male births) from either the source or local population.

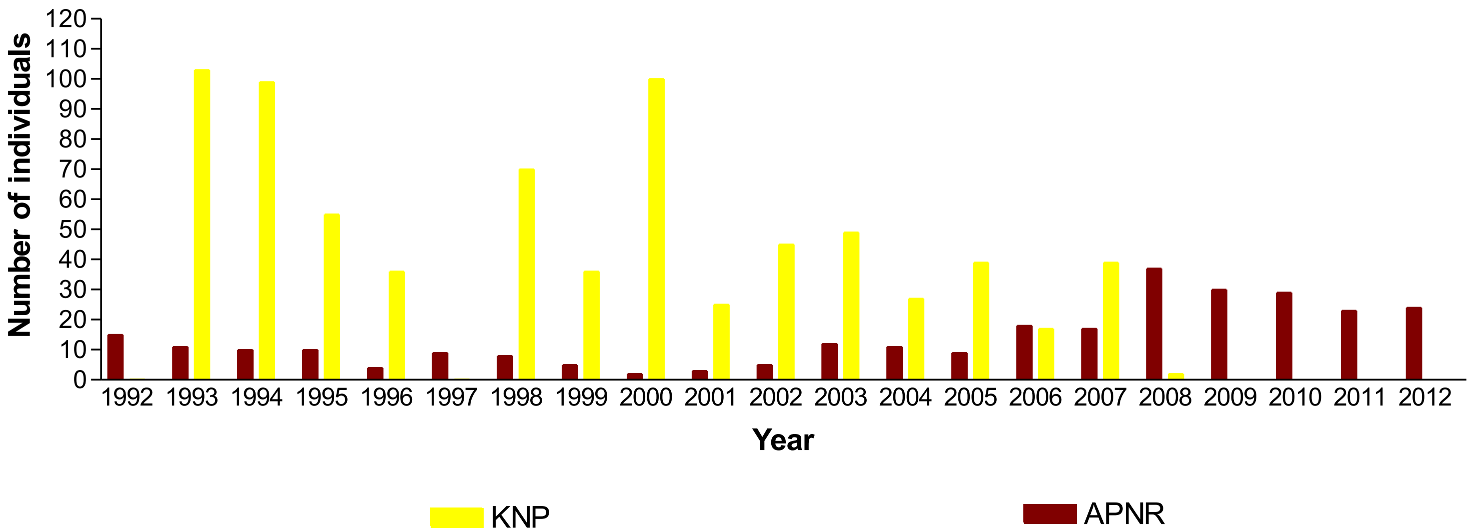

Figure 4. The number of elephant deaths, irrespective of the sex or cause of death for comparative reasons, recorded within the APNR and KNP over the past 20 years. Numbers for the KNP in recent years are currently unavailable while in these same years (from 2008 onwards) mortality figures in the APNR have increased compared to earlier years.

Mortalities due to anthropogenic influences represent the greatest cause of mortality for elephants within the APNR and constitute 78% of all mortalities recorded over the 20 year period (Figure 5). Of the mortalities ascribed to anthropogenic influences, trophy hunting represents the greatest cause of death to elephant bulls in the young adult to prime age categories. Within the Balule-, Klaserie-, Timbavati- and Umbabat Private Nature Reserves, trophy hunting has constituted 69%, 93%, 76% and 78% of all deaths due to anthropogenic influences with an overall contribution of 80% across the APNR.

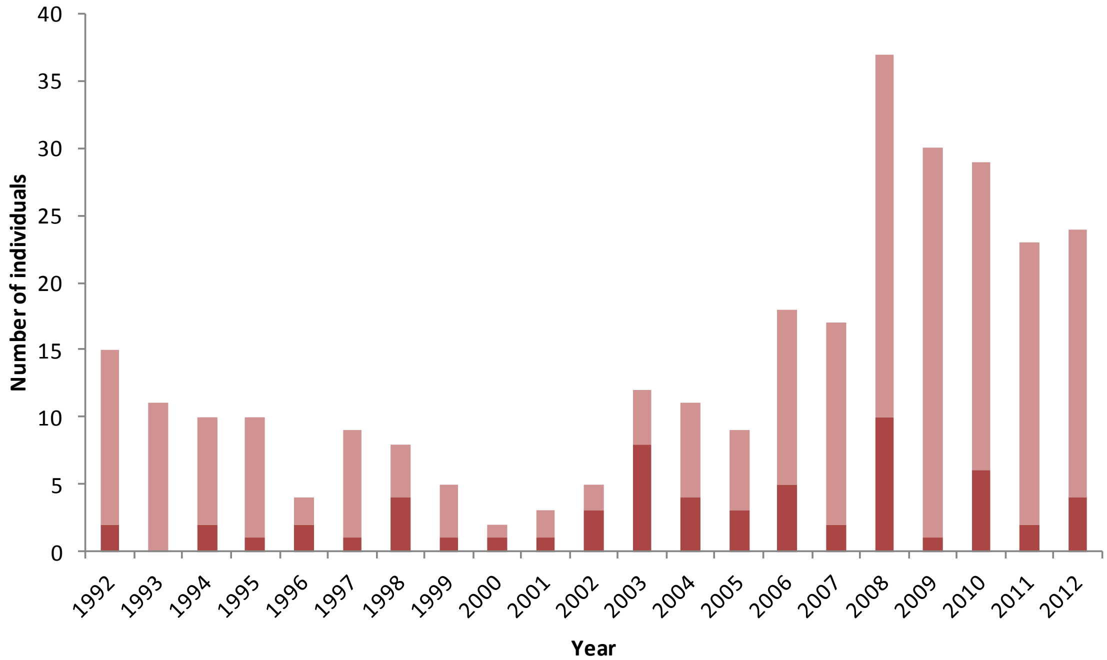

Figure 5. The proportion of elephant mortalities within the APNR which are either due to anthropogenic influences (light red) or natural causes (dark red).

Mark Resight models for estimates of abundance

Analysis of collared elephant's data indicated that animals rarely dispersed from within the APNR to the KNP which proved to be important information required for model development. Depending on the age group under consideration, animals were found to temporarily either immigrate into or emigrate from the APNR. The temporary immigration and emigration patterns in the collared elephants which were incorporated into the model development, were based on the premise that collared individuals movements were indicative of the population's movements as a whole. After pooling the amount of locations outside of the APNR within a month and across all individuals within a specific age category, it was evident that bulls of certain ages spent more time outside of the APNR in particular months (Figure 6&7). Immature and adult age categories appeared to have no particular preference for a specific time of year and both these age categories spent on average approximately one quarter of their annual radio- tracked time (three months) outside of the APNR Young adult-, prime and senescing bulls appeared to spend more time outside of the ANPR in the drier months when compared to other times of year. In general prime bulls had high frequencies of locations outside of the APNR which could add up to six months of the year, young bulls to four months of the year and senescing bulls spent on average only three months of the year in either of the Reserves (KNP or APNR). Individual heterogeneity in movement patterns was observed which was most prevalent in the older age classes as movements between particular reserves were largely dependent on annual musth cycles and the return to non-musth ranges which are likely to tie in with a bulls' place of origin. Genetic studies are underway to establish what genetic components can be linked to particular movement patterns.

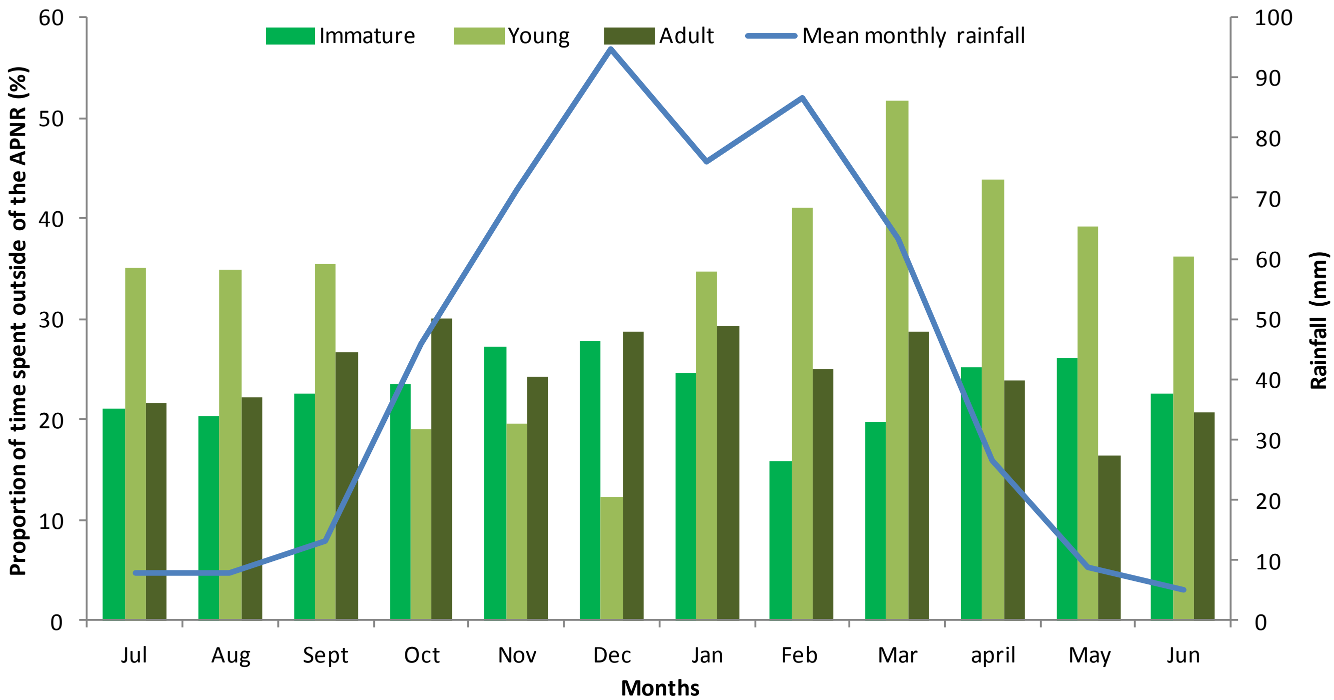

Figure 6. The proportion of GPS locations found outside of the APNR for the immature (n=11), young (n=4), and adult (n=8) radio-collared bulls that don't yet experience regular annual musth cycles. GPS locations of collared females were also included in the analysis for the immature age category as most immature males will still be socially dependent on their natal family units and will therefore be in close proximity to them. Mean monthly rainfall was collated from three weather stations within and in close proximity to the APNR (i.e. Ingwelala, Hoedspruit Airforce Base and Kingfisherspruit).

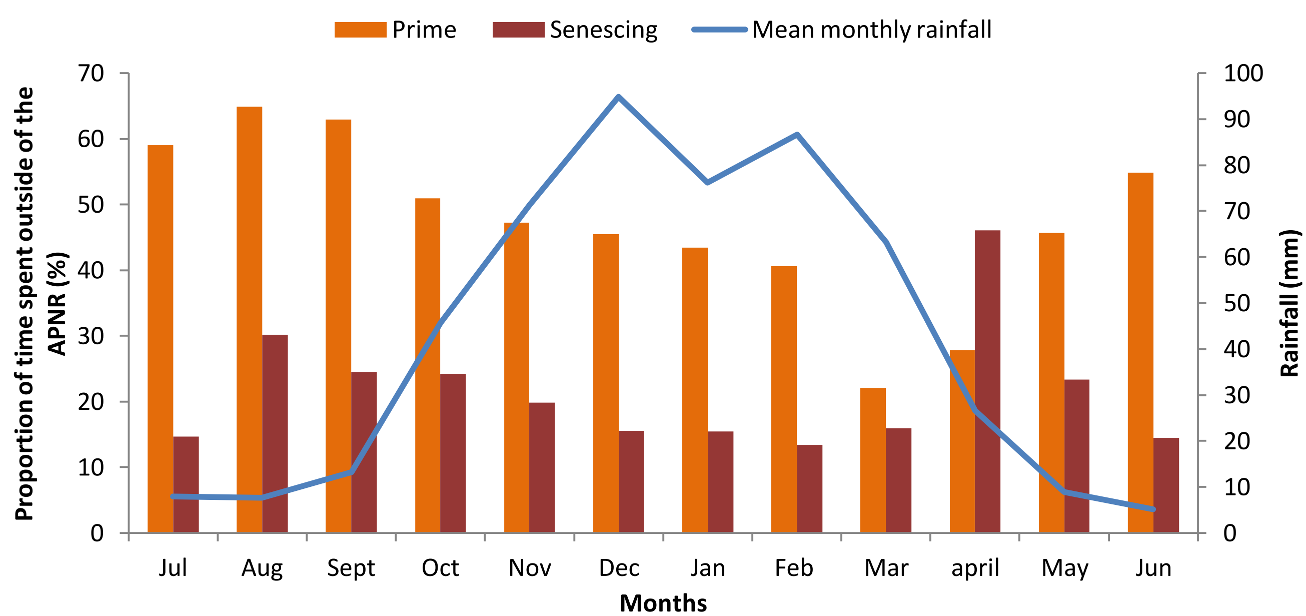

Figure 7. The proportion of GPS locations found outside of the APNR for the prime (n=9) and senescing bulls but which still have regular annual musth cycles (n=2).

Estimates of abundance for the entire bull population

Both the JS and IELNE models require information on resighting events in year *t*+1 in order to provide estimates for year *t*. Hence population estimates were only available until year 2010, using the 2011 data to arrive at these estimates. The RD model does, however give an estimate for every year. As the IELNE represents the most sophisticated model with the largest data input file which requires many iterations of runs to arrive at a result, only approximately 1% of processing time was completed after 8 hours of processing time. This model is currently still running and the pending results could therefore not be incorporated in this report. The remaining model outputs compared favourably with the census results showing similar trends when considering the estimates for all bulls using the JS and RD model outputs. Irrespective of the technique that was used to derive the estimates, a decline in numbers in the bull segment of the APNR is visible for 2009 (Figure 8). The KNP bull population estimate did increase with approximate 100 individuals over this same period which does imply that a more than the usual amount of bulls could have moved out of the APNR over this time. It would appear as if most emigration occurred within the young bull population (Table 2). It is interesting to note that the year preceding this emigration event, elephant mortality figures were higher than usual within the APNR i.e. natural mortality numbers were at their highest while mortality due to anthropogenic events such as trophy hunting had also sharply increased (Figure 5). These results provide some evidence that fluctuations in elephant abundance figures can be sensitive to disturbance events occurring the year prior to obtaining the abundance estimate.

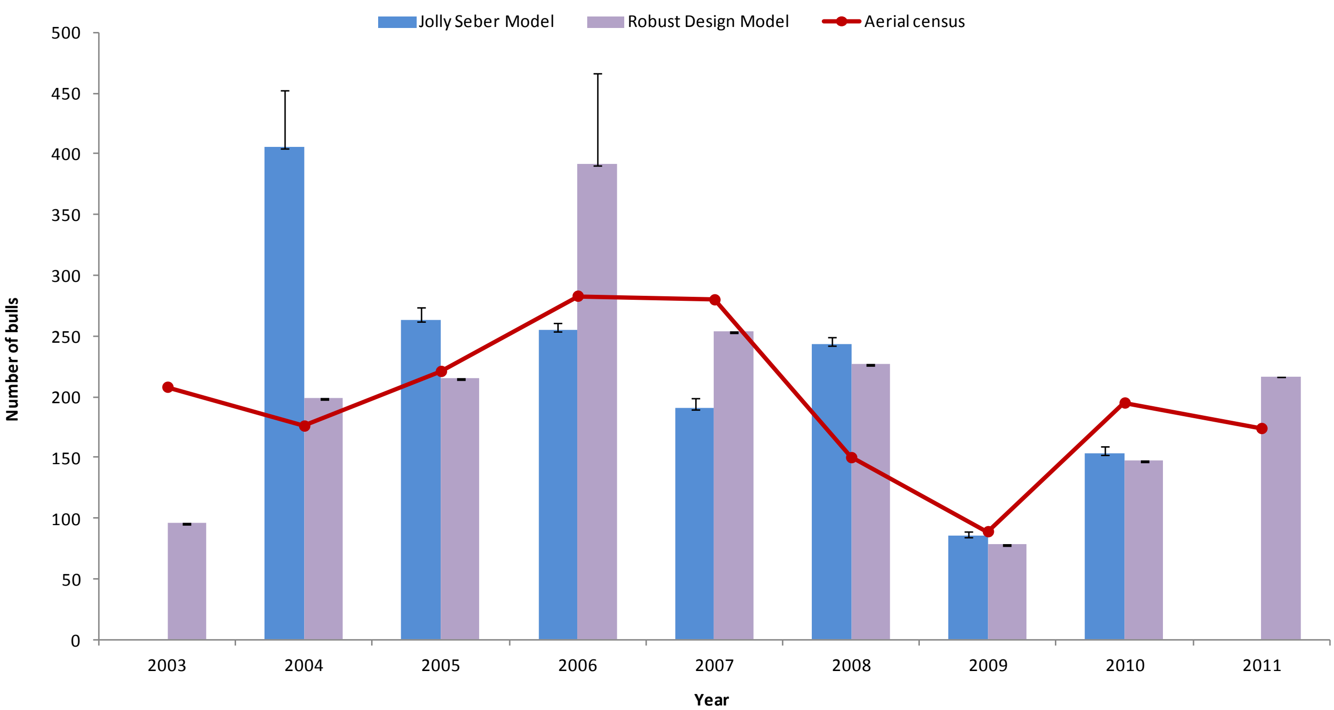

Figure 8. Population estimates for the bull segment of the APNR elephant population using the Jolly Seber-, Robust Design Models and the annual aerial census counts. Estimates obtained from the models for 2003 only represented a half a year as the study officially started in May 2003.

Estimates of abundances per age group

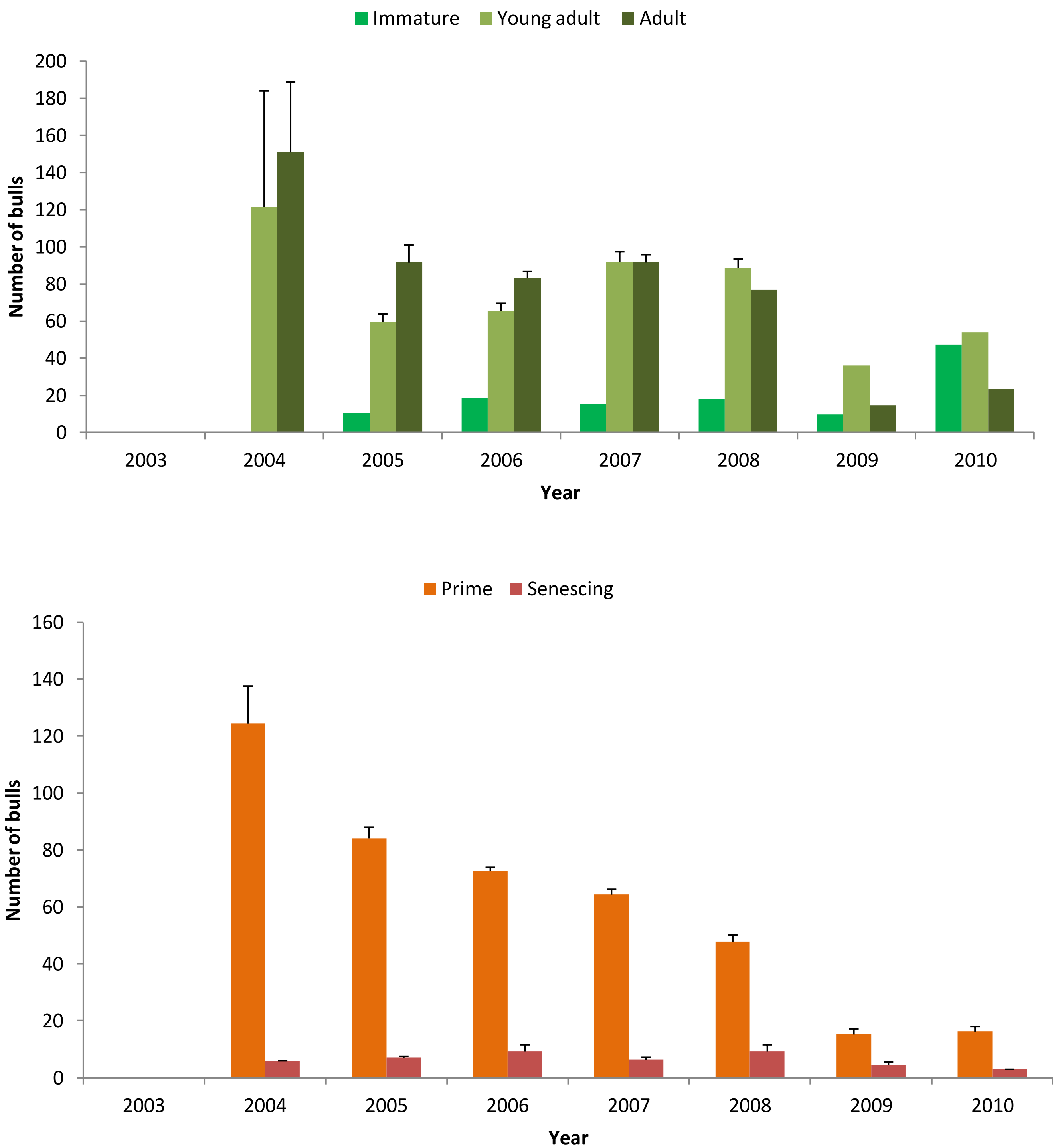

Figure 9. Changes in abundance estimates derived via the JS model for each of the age groups under consideration. The figure with green column bars refers to those bulls that haven't experienced regular annual musth cycles while the figure with warm coloured provides estimates for the older segments of the bull population within the APNR and whose individuals experience regular annual musth cycles which may lead them outside of the APNR.

The results from the model runs for each of the age categories are in agreement with the general trend in census information according to which there are indications of a decline in the overall bull population from 2008 onwards for both the APNR and KNP populations (Figure 1). It is evident that these declines are most prevalent within the adult, prime and senescing cohorts of the APNR population (Figure 9 and Table 2). However, there has been a slow but steady attrition of prime bull numbers within the APNR which has been occurring since the inception of the study and which has been reported earlier (Henley & Henley 2008). These fine scaled trends relating to mark-recapture models serve to emphasise the value of a technique that can distinguish between different age groups of animals that would otherwise not have been possible from annual aerial census techniques, especially for young bulls found within breeding herds. As mentioned by Stalmans (2003), if animals are being harvested at an order of magnitude of 1-2% per year, any slow attrition in numbers may not be detected on an annual basis by a technique that returns data at a coarser demographic resolution.

Table 2. Estimates of abundance using the JS model (estimate ± SE) for the immature, young adult, adult, prime adult and senescing age categories of elephant bulls found within the APNR.

Year	Immature	Young	Adult	Prime	Senescing	TOTAL[1]
2003	0	0	0	0	0	0
2004	0	121 ± 63	151 ± 38	124 ± 13	6[2]	406 ± 47
2005	11	60 ± 4	92 ± 10	84 ± 4	7	263 ± 11
2006	19	66 ± 4	83 ± 4	73 ± 1	9 ± 2	255 ± 7
2007	15	92 ± 6	92 ± 4	64 ± 2	6 ± 1	191 ± 8
2008	18	89 ± 5	77	48 ± 2	9 ± 2	243 ± 6
2009	10	36	15	15 ± 2	5 ± 1	85 ± 5
2010	47	54	23	16 ± 2	3	154 ± 6

[1] *The total as calculated by the model and not the sum of the respective cells*
[2] *Standard errors that round to zero are not included in the table*

Survival analysis

The goodness-of-fit test of the resight data gathered from all elephant bulls indicated that the data showed some deviations from the CJS model assumptions which are probably due to unequal chances of resight probability among individuals. Such deviations tend to have a small impact on the point estimates but rather influences variance estimates. Survival and resight probability was year-dependent when all bulls combined were considered, with the most parsimonious model including these time effects (Table 3, model 1). There was substantial variation in survival probability over the study period from 62% in 2007 to 94% in 2003 (Figure 10).

Table 3. Model selection for survival analysis in elephant bulls. (Phi represents annual survival; p=annual resight probabaility; t=time-dependent; .=constant)

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(t)p(t)}	3396.6106	0	0.94476	1	15	480.0932
{Phi(.)p(t)}	3402.2891	5.6785	0.05524	0.0585	9	497.9786
{Phi(t)p(.)}	3442.8899	46.2793	0	0	9	538.5793

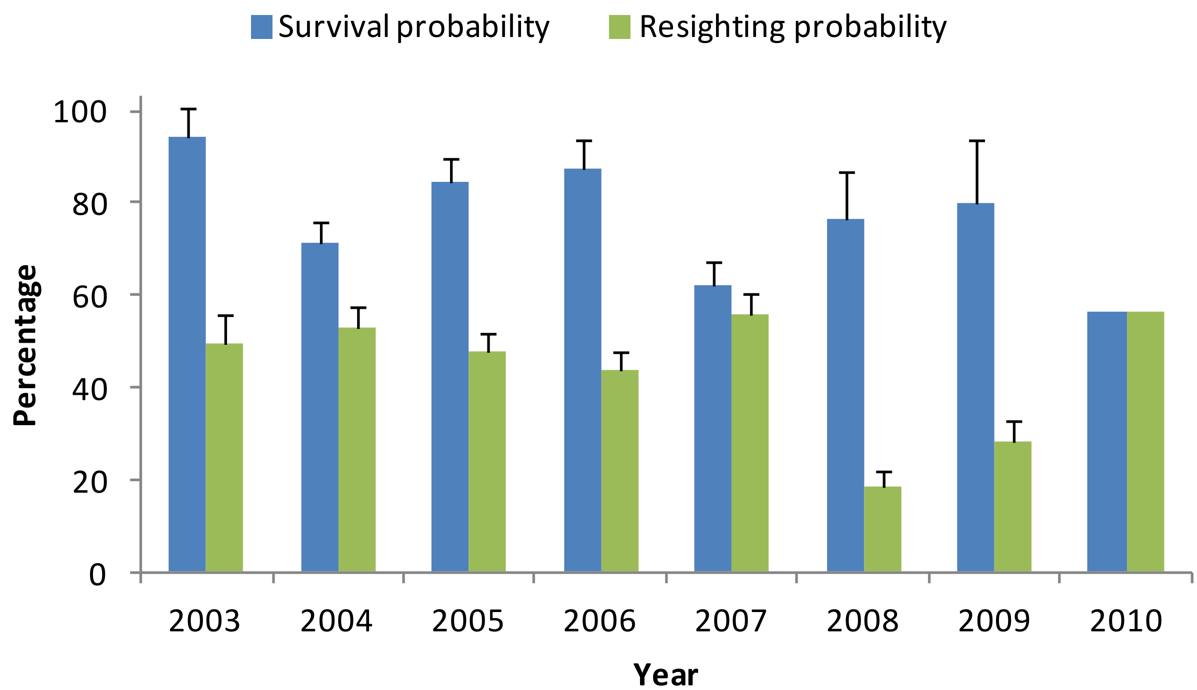

Figure 10. The survival (Phi) and resight probability (p) over all bulls for the best fit time/year-dependent model.

Over the study period mean annual survival and resight probability of all bulls were 86.6% (SE ±0.034) and 52.2% (SE ±0.055) respectively.

Although still indicating departure from model assumptions, the goodness-of-fit test results improved when data was categorised according to elephant age group (Chi square=173.3, df=92, P<0.01) but in this instance group/age had a significant effect on survival but no year effects were apparent (possibly due to lower sample sizes in each of the groups). The reverse applied when considering the resight probability (Table 4). Overall, older animals appeared to have higher survival probabilities than younger ones (Figure 11). However, any elephant permanently moving out of the study area will be interpreted as a permanent mortality under the CJS model. Survival within a mark-recapture context is often referred to as ‘apparent survival’ which involves both real survival rates and permanent emigration. Bulls in the senescing age category’s higher survival probabilities are in all likelihood linked to their site fidelity as they no longer come into musth and ‘retire’ to so-called bull areas.

Table 4. Model selection for survival analysis in elephant as per age category

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(g.)p(t)}	3383.16	0	0.75829	1	13	950.8681
{Phi(g.)p(gt)}	3385.447	2.2867	0.2417	0.3187	44	888.6258
{Phi(gt)p(gt)}	3407.399	24.2385	0	0	74	845.3995
{Phi(.)p(t)}	3410.104	26.944	0	0	9	985.9387
{Phi(g.)p(g.)}	3475.473	92.3127	0	0	10	1049.28

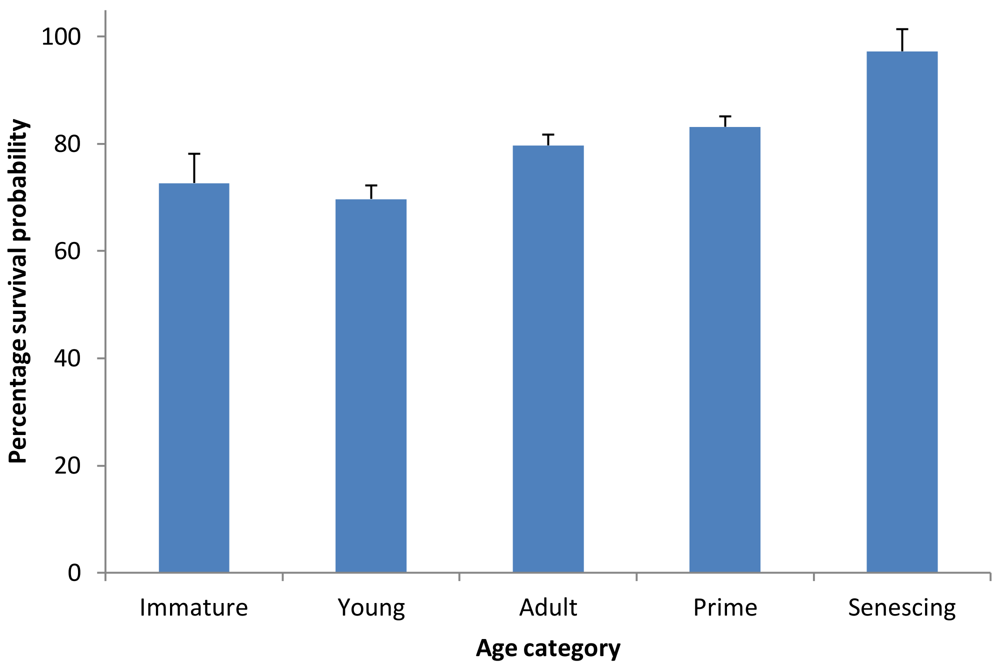

Figure 11. Survival probabilities for bulls per age category

When considering the survival rates of bulls with tusks of approximately 80lbs, no difference could be found in the constrained model type or results that were developed when analysing survival and resighting probabilities over all bulls. Small sample sizes meant that the data deviated from CJS models (Chi square=10.9, df=16, P=0.183).

Based on the decline detected in the overall adult bull population when considering the aerial census results, data was grouped into two periods of four years each (2003-2007 and 2008-2011) The resulting good model fit ({Phi(2 periods.)p(t)} Model AICc=3397.12; Delta AICc=0.5091) produced a decline in survival rate of 10% between the two periods (81.7 ±1.75 SE for the first period as opposed to 71.7±2.79 SE during the last four years) which corroborates the findings of other abundance estimates. These declines in abundance figures and survival probabilities within the bull segment of the APNR population could either be due to real increased mortality events or dispersal in association with density dependence factors which may come into play and be driven by the expanding Kruger population.

RECOMMENDATIONS

Suggested off-take proportions for elephant bulls have varied regionally (Table 5). The APNR has implemented some of the highest hunting quotes suggested (principle of 2%). As demographic analyses of the population has revealed a downward trend in the prime bull cohort of the population over a number of years, management should err on the side of caution in terms of proposed off-takes, especially within this segment of the population as they are less abundant and socially important within elephant society.

To incorporate the effects of mortality on the demography of the bulls and the population at large, continual submittal of clear ear identification photographs of all dead elephants should be maintained. To monitor the effects of trophy hunting on tusk size, sustained effort should be made to link all ages collected from the measurements of the lower jaws of dead elephants to tusk weights.

Table 5. Information on hunting quotas set within different regions of Africa for African elephants.

Percentage	**Region**	**Description**	**% of total pop.**
Barnett & Patterson (2006)	Zimbabwe	Revision of Martin & Thomas recommendation by Department of National Parks and Wildlife Management	< 0.5%
Caughley (1993).	Overall	The Maximum Sustainable Yield (MSY) for elephant is approximately half the population's maximum rate of increase, multiplied by half the size of the population when not harvested.	MSY
Caro *et al.* (1998)	Tanzania-Selous	No apparent detrimental effect on the population over five year period	0.06 %
Craig et al. (2011)	Overall	Quotas typically set by managers	≈0.5%
Craig et al. (2011)	Botswana	From trophy hunting records from 1996-2010, maximum of 0.2 % in 2009	<0.2%
Craig et al. (2011)	Botswana	Hunting quotas in excess of this percentage will lead to a loss of highly desirable tusks in excess of 70lbs	<0.35%
De Villiers & Funston (2004)	APNR	Bulls older than 30 years with a mitigating factor, the actual bulls hunted must be older than 50 years and have tusks less than or equal to 70 lbs.	< 3.6%
Martin et al. (1997)	Zimbabwe	To sustain good quality trophies	< 0.7%
Martin & Thomas (1991)	Zimbabwe	History of effective and sustained utilization of wildlife outside of protected areas under The Zimbabwe Campfire Program	< 0.75%

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