

## RESEARCH

---

# Growth characteristics of tusks of elephants in Kruger National Park

Ian J Whyte<sup>1\*</sup> and †Anthony Hall-Martin<sup>1,2</sup>

<sup>1</sup>South African National Parks, Private Bag X402, Skukuza 1350. South Africa.

<sup>2</sup>African Parks Network.

†A. Hall-Martin passed away May 2014. (see Obituary: *Pachyderm* Vol. 55)

\*email: ian@mpu.co.za

### Abstract

Two historic data sets on various tusk growth parameters were examined from African savanna elephants (*Loxodonta africana*) from the Kruger National Park (KNP), Republic of South Africa. Data were collected from a sample of 1,555 elephants culled randomly. In both data sets, the age and sex of the animal was known. In the first set, tusk mass, length, circumference and pulp cavity volume had also been recorded, while in the second, only tusk mass was recorded. Analysis of the data showed, as expected, significant differences between growth parameters of tusks in males and females. In males, tusks were significantly larger. Longitudinal growth in males was found to be constant throughout life, as was the expansion in circumference. Dentine was therefore deposited throughout life at an accelerating rate, resulting in accelerating mass increase in the tusks. In females, however, tusk growth apparently ceased at about 40 years of age. After this age, tusk circumference and length remained relatively constant while mass and length decreased, probably due to breakages and wear. The incidence of tusklessness and of single-tusked animals of each sex in the population was low, and the evidence suggests that the lack of tusks was mostly the result of accidental injury, not genetic inheritance. Estimates of the incidence of laterality showed that slightly more elephants were 'right-tusked' than 'left-tusked'. These results from a large sample of elephants from KNP will contribute to understanding of differences among African elephant populations and the extent to which these are genetically and/or environmentally determined.

### Résumé

Deux jeux de données historiques regroupant différents paramètres de croissance de défenses ont été examinés chez des éléphants de savane d'Afrique (*Loxodonta africana*) du Parc National Kruger (PNK) en Afrique du Sud. Les données ont été recueillies sur un échantillon de 1.555 éléphants sélectionnés au hasard. Dans les deux ensembles de données, l'âge et le sexe de l'animal étaient connus. Dans un premier ensemble, la masse, la longueur, la circonférence et le volume de la cavité de la pulpe avaient également été enregistrés, alors que dans le second cas, seule la masse de défense était enregistrée. L'analyse des données a montré, comme prévu, des différences significatives de croissance des défenses entre les mâles et les femelles. Chez les mâles, les défenses étaient significativement plus grandes. La croissance longitudinale chez les mâles s'est avérée constante tout au long de la vie, tout comme l'expansion de la circonférence. La dentine s'est déposée tout au long de la vie à un rythme accéléré, entraînant une augmentation accélérée de la masse des défenses. A contrario chez les femelles, la croissance des défenses semble cesser vers l'âge de 40 ans. Après cet âge, la circonférence et la longueur des défenses sont restées relativement constantes, tandis que

la masse et la longueur ont diminué, probablement en raison de casse et d'usure. L'incidence d'absence de défense et de défense unique pour chaque sexe était faible dans la population, et les preuves suggèrent que le manque de défenses résulte principalement d'une blessure accidentelle et non d'un héritage génétique. Les estimations d'incidence de latéralité ont montré que les éléphants étaient légèrement plus «droitiers» que «gauchers». Ces résultats obtenus à partir d'un large échantillon d'éléphants du PNK contribueront à la compréhension des différences entre les populations d'éléphants d'Afrique et à la mesure dans laquelle celles-ci sont génétiquement et/ou écologiquement déterminées.

---

## Introduction

From earlier population studies based on data derived from randomly culled African savanna elephants (*Loxodonta africana*) in the Kruger National Park (KNP), two unanalysed data sets still existed on tusk growth parameters. In both data sets, the age and sex of the animals were known. In the first set, collected by Hall-Martin, tusk mass, length, circumference and pulp cavity volume were recorded; while in the second Whyte recorded only tusk mass.

These data allowed the formulation of some research questions: To what extent and in what respects do the various growth parameters differ between the sexes? Do elephants show any laterality in the use of their tusks, i.e. are elephants predominantly 'left-tusked' or 'right-tusked'? What is the incidence of tuskless and single-tusked animals in the KNP population? Lastly, what evidence is there to suggest that 'tusklessness' is genetically transferred?

Although many papers have been written on elephants' tusks, for example on their morphology (Raubenheimer et al. 1995), morphometry (Elder 1970), aspects of their chemical composition (e.g. Lee-Thorpe et al. 1991), structure (e.g. Raubenheimer et al. 1990), and laterality (Bielert et al. 2017), little attention has been given to tusk growth characteristics. This may be ascribed to the lack of data on the age of elephants from which most studies of elephants' tusks have been conducted, without which growth rates cannot be described. Laws (1966) did relate tusk growth in mass to age, as did Pilgrim and Western (1986), but in both cases with a view to inferring sex and age from tusk measurements. Perry (1954) was of the opinion that tusks of females ceased to grow after puberty, while in males the rate of tusk growth was retarded after puberty. Laws (1966) and Sikes (1971) refuted these conclusions, suggesting that in females growth is linear and

continuous, and that in males the rate of tusk growth increases progressively throughout life.

In this study we compared our results with the conclusions of these authors and found distinct differences. Growth parameters showed marked sexual dimorphism, and insights into laterality (left- or right-tuskedness) and the incidence of tusklessness and single-tuskedness were also gained from the data. The data sets used in this study are probably unique in that individual tusks were from elephants whose sex and age were known, and this study breaks new ground by developing mathematical descriptions of the growth patterns.

## Materials and methods

The Kruger National Park (KNP) is located at the north-eastern corner of the Republic of South Africa (RSA) along its eastern border with Mozambique. It covers an area of 18,992 km<sup>2</sup>, and lies between latitudes 22° 20' and 25° 32' S and longitudes 30° 53' and 32° 02' E. Between 1967 and 1994, African savanna elephants were routinely culled in KNP due to the perceived need to maintain the population at around 7,000 in order to limit their impact on certain elements in the vegetation (Pienaar et al. 1966, van Wyk and Fairall 1969). Data from this study were derived from some of these culls. Whole family units, selected at random from the population, were culled, allowing the assumption that the data are representative of the larger KNP population. Two historic data sets were available for analysis in this study. The first was from 230 animals (104 males and 126 females) culled between 1979 and 1981. This data set was collected by Hall-Martin, and various measurements were taken of tusks including mass, length, circumference and volume of the pulp (nerve) cavity. Ages of animals ranged between 2 and 57 for females and 2 and 55 for males. The second, larger data set was collected by Whyte from 1,340 animals (605 males and 735 females) culled between 1989 and 1996, when only the mass of the tusks and ages of the animals were available. Ages of females in this set ranged between 2 and 60 and those of males between 2 and 55. The age against tusk mass analyses

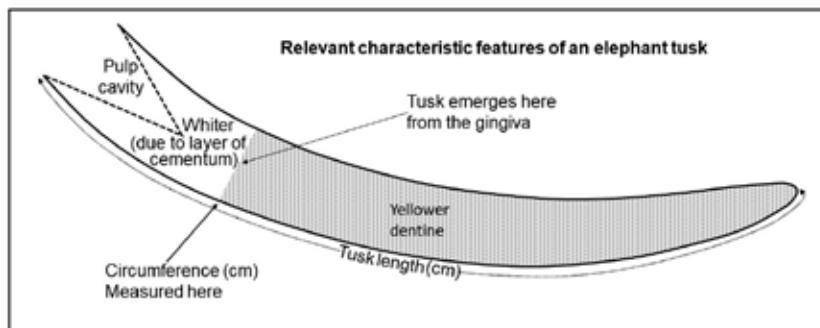


Figure 1. Relevant characteristic features of an elephant tusk.

included 1,555 animals both data sets, of which 709 were males and 846 were females. Data from calves which had not yet developed tusks were not included in either data set.

Unfortunately, no information on the condition of the tusks was recorded. Some tusks may have been excessively worn or broken, but only the age of the animal and the mass of its respective tusks were recorded. Lighter tusks may thus have been broken, but this could not be inferred from the data. Breakages would account for some, perhaps most, of the variation in the tusk weights of animals of a similar age.

Tusks were chopped out of the alveoli of the fresh elephant carcasses and weighed immediately to the nearest 0.1 kg. Tusk length was measured in centimetres along the outside curve of the tusk from the edge of the base to the tip. The circumference was measured at the gingiva (Fig. 1). The whiter colour of the tusk in the alveolus due to a thin cementum layer (Raubenheimer et al. 1990) and the exposed yellower dentine (shaded grey) allowed this position on the tusk to be easily determined.

The volume of the pulp cavity was measured to the nearest millilitre by filling the cavity with water and then pouring this into a measuring cylinder.

Ages of culled elephants were determined from replacement and wear on the mandibular molars according to the method of Laws (1966). Mandibles were stored in a scavenger-proof open-air facility. Each had a metal tag with its unique sequential number attached with wire to the mandibular condyle for later age determination. The ages of all elephants in the sample were estimated by the first author.

In all analyses, data from the greater of the measurements from the two respective tusks of

each animal was used so as to minimise errors induced by abrasion and breakages. In all analyses, mass and dimensional parameters were simply plotted against age. Data for males and females were analysed separately. To allow for possible comparisons with similar tusk data from other populations, regression analyses were conducted on

all of the growth parameters. Least squares regressions were used for linear relationships, while nonlinear regression analyses included multiplicative models (of the form  $Y = aX^b$ ) and, for asymptotic growth curves, Gompertz equations of the form  $Y = ab^{t^n}$  (du Toit and Herbst, 1981). All of these models were fitted to each data set, and the one yielding the best correlation was used. An  $F$ -test of the linear regression analyses of log-transformed tusk mass and age data was used to test for differences in growth in tusk mass between male and female elephants.

Laterality was determined through the tusks weights. It was assumed in this study that the lighter tusk was the 'working' tusk (doing more of the debarking and digging), which therefore experienced more wear, and indicated right- or left-tuskedness. Data for tusklessness and single-tusked elephants came only from the 1989–96 data set as all culled animals were sampled regardless of whether they had tusks or not. In the earlier data set, tuskless animals were ignored. Although absence of a tusk or tusks may have been the result of injury, this could not be confirmed through inspection of the skulls, as they were destroyed through processing into carcass meal.

## Results

### *Sexual dimorphism*

In all of the measurements taken, clear sexual dimorphism was apparent. In males, tusk growth continued through to the oldest animal sampled (55 years) while in females, growth apparently either ceased between the ages of 40 and 45 years, or else was offset by breakages and wear. The regression equations for all the respective growth parameters (tusk mass, length, circumference and pulp cavity volume) are given in Table 1. An  $F$ -test on the slopes of the linear

Table 1. Best-fit models of growth parameters of tusks of elephant males and females from Kruger National Park, based on analysis of tusks from 1,555 elephants culled in 1979–81 and 1989–1996. PCV: pulp cavity volume;  $y$ : growth characteristic;  $x$ : age in years;  $r$ : correlation coefficient (\*indicates that value for  $r^2$  is shown);  $n$ : sample size; SE: standard error.

Growth parameter	Model	Equation	$r$	$n$	SE
Mass (females): 2–40 yr	Linear	$y = -0.155 + 0.133x$	0.896	759	-
Mass (females): 40–60 yr	Linear	$y = 6.229 - 0.018x$	-0.096	99	-
Mass (males): 2–55 yr	Multiplicative	$y = -2.788x^{0.612}$	0.96	709	0.319
Length (females): 2–57 yr	Asymptotic	$y = (113.745 \times 0.193)^{0.906x}$	0.86*	126	-
Length (males): 2–6 yr	Linear	$y = 4.06 + 9.756x$	0.873	21	-
Length (males): 6–55 yr	Linear	$y = 28.53 + 4.296x$	0.946	85	-
Circumference (females): 2–57 yr	Asymptotic	$y = (24.662 \times 0.383)^{0.933x}$	0.87*	126	-
Circumference (males): 2–55 yr	Multiplicative	$y = 2.063x^{0.443}$	0.954	104	0.109
PCV (females): 2–41 yr	Linear	$y = 97.32 + 10.8x$	0.761	118	-
PCV (females): 41–57 yr	Linear	$y = 1369.67 - 20.09x$	-0.667	10	-
PCV (males): 2–55 yr	Linear	$y = 297.61 + 105.47x$	0.892	104	-

regression analyses of log-transformed tusk mass on age confirmed a highly significant difference between males and females ( $F = 527.8$ ,  $p < 0.0001$ ). The regression equation for females was  $y = 1.08 + 1.11x$  ( $p < 0.001$ ,  $r^2 = 0.89$ ) and for males,  $y = 1.21 + 1.61x$  ( $p < 0.001$ ,  $r^2 = 0.93$ ).

### Tusk mass

In females, the increase in the mass of tusks was linear until 40 to 45 years (Table 1, Fig. 2a). A linear regression analysis on data from females older than 40 years yielded a significant negative correlation, showing that the weight of females' tusks declined from this age onwards, probably due to breakages and wear. The heaviest tusk recorded from a female was 8.7 kg from a 37 year old. One female of 58 years had tusks far larger than any other (10.7 and 8.4 kg), but as she had never had a calf and showed male characteristics, her data were excluded from these analyses.

In males the increase in the mass of tusks with age was not linear but increased at an accelerated rate throughout life. A multiplicative model of the form  $Y = aX^b$  gave the best fit to these data (Table 1, Fig. 3a).

### Tusk length

As with tusk mass, growth in tusk length in female elephants ceased between 40 and 45 years of age (Table 1, Fig. 2b), but while tusk mass declined thereafter, there was little evidence that tusk length

declined (see 'Discussion'). The relationship between age and tusk length was therefore asymptotic and a Gompertz model of the form  $Y = ab^{ct}$  was used. Mean asymptotic tusk length for females was 113.7 cm. The longest tusk recorded was 144 cm from a 45 year old.

In males, growth in length showed two phases both of which were linear. There was an initial rapid increase in length from two to six years old followed by a slower, but still linear increase which persisted until at least 55 years, the age of the oldest male in the sample (Table 1, Fig. 3b). Variables for the model equations are given in Table 1. The longest tusk recorded from a male was 264 cm from a 55 year old.

### Tusk circumference

The relationship between age and tusk circumference in females was also asymptotic and again the Gompertz model was used (Table 1, Fig. 2c). Mean asymptotic tusk circumference was 24.7 cm. The thickest tusk recorded from a female had a circumference of 32 cm from a 55 year old.

The circumference of tusks in males also showed an increase throughout life, but this increase with age was not linear (Table 1, Fig. 3c). A multiplicative model ( $Y = aX^b$ ) was used for the analysis. The thickest tusk recorded from a male had a circumference of 48 cm from a 38 year old.

### Pulp cavity volume

In females, changes in the volume of the pulp cavity over time showed two phases both of which were linear.

There was an increase from two to 41 years old followed by a linear decrease (as it filled with secondary dentine), which persisted until 57 years (Table 1, Fig. 2d). The largest tusk pulp cavity volume recorded from a female was 785 ml from a 41 year old.

The pulp cavity of tusks of male elephants increased linearly throughout life (Table 1, Fig. 3d). The largest tusk pulp cavity volume recorded from a male was 6,000 ml from a 38 year old.

### Laterality

Differences in mass between the left and right tusks of an elephant are common and indicate whether the animal was left-tusked or right-tusked, based on the assumption that the working tusk is lighter due to increased abrasion. In the total sample, 471 (30.3%) animals showed no laterality (tusk weights were equal). Of these 'ambidextrous' animals, 200 were males and 271 were females. The majority of these were in the younger age classes but lack of laterality occurred throughout the age classes. The oldest ambidextrous female and male were 55 (4.0 kg tusks) and 37 (20.0 kg) years old respectively.

Of those showing laterality, more left tusks were heavier than right. In males the ratio was 249:210 ( $\chi^2 = 3.31$ ,  $p < 0.1$ ), while in females it was 275:241 ( $\chi^2 = 2.24$ ,  $p < 0.5$ ). When the samples were combined, the sample size was large enough to show a significant difference ( $\chi^2 = 5.47$ ,  $p < 0.025$ ). Slightly more elephants thus have heavier left tusks than right, indicating a preponderance of right-tuskedness.

### Tusklessness

Of the total of 1,340 elephants sampled for which data on absence of tusks was available (i.e from the 1989–96 data set), 15 (1.1%) were tuskless. All of the tuskless animals were females whose ages ranged between 9 and 52 years (see Table 2). The youngest tuskless animal in the sample was nine years old. Tuskless males do occur in the

population (Whyte pers. obs.), but no data exist on the frequency of the occurrence, and none were encountered in the culled samples.

### Single tusked animals

Single-tusked animals were from both sexes. Fifteen males out of 605 from the 1989–96 data set and 35 females out of 720 were single-tusked. A significantly higher proportion of females than males were recorded with only one tusk ( $\chi^2 = 4.50$ ,  $p < 0.05$ ), but there was no significant difference between the number of times that such tusks were recorded on the left or right side. Ages of single-tusked females ranged from 7 to 41 years and those of males from 8 to 55 (Table 2). All elephants under the age of seven ( $n = 193$ , 12.4% of the sample) had both tusks.

## Discussion

The two historic data sets, consisting simply of a few basic parameters pertaining to the tusks of elephants whose ages were also known, provided useful insights into the patterns of tusk growth in male and female elephants from KNP. Many of the results of the study would have been intuitively expected; for example, the stark differences between tusks of male and female elephants are very evident even to a non-expert. This study confirms that there is clear sexual dimorphism in all aspects of tusk growth, with the major difference being that male tusks are significantly larger than females. Moreover, in females, tusk growth appears to cease at about 40 years old; this however was an unexpected result.

For males, the results of this study concur with the conclusions of Laws (1966) and Sikes (1971) that the rate of tusk growth in males increases progressively throughout life. In KNP males, continuous growth both longitudinally and in tusk girth at the alveolus resulted in accelerated deposition of dentine. Thus the mass of the tusk also increased at an accelerating rate, with the major weight gain occurring late in life.

For females, our findings differ from those of both

Table 2. Occurrence of single-tusked elephants in Kruger National Park, based on analysis of tusks from 1,325 elephants culled in 1989–1996.

Missing tusk	Females (n = 720)	Males (n = 605)	Total (n = 1,325)
Left	13	6	19
Right	22	9	31
Total	35	15	50

Laws (1966) and Sikes (1971), who considered that growth of female tusks was continuous throughout life, and Perry (1954) who argued that the tusks of females cease to grow after puberty. In KNP females, tusks ceased to grow at an age of around 40 years (not at puberty). Growth in length and girth were constant from birth until around 40 years of age. Thereafter, no further increase in girth occurred, while tusk mass declined, apparently due to wear and breakages. Tusk length also declined after 40 years, but the decline was minimal. This may be due to wear on the lateral surfaces of the tusks particularly at the tip where wear would presumably be greatest. This pattern of wear would affect mass more than it would length. Unfortunately, it was only in the analysis that this anomaly became evident, and no data were collected on tusk tip profiles, which could either confirm or refute this.

Detailed analysis reveals further differences in growth parameters between males and females. Males' tusks grow longitudinally in two distinct phases. There is a primary growth spurt for the first five or six years followed by slower growth, which continues throughout life. There are two possible reasons for the two growth phases. The tusk of the elephant represents a maxillary incisor and is preceded by a primary deciduous tooth or tush (Raubenheimer et al. 1995; Sikes 1971). It may be that this primary tush grows at a faster rate than the secondary tusk, or else younger elephants have not yet begun to use their tusks, which means that tusk abrasion is limited. This may occur in females also but the two growth phases were not evident from the analyses, possibly due to the much slower growth rates of their tusks. This phenomenon also only became apparent during data analysis, and it thus has received no detailed attention.

Our data also show that the pulp cavity of the tusks of females begins to close at about 40 years. This seems to be a similar process as occurs in the canine teeth of the larger cats such as lions (Smuts, Anderson and Austin, 1988). Once the tusks have become established, growth ceases and the cavity slowly closes as it fills with secondary dentine. Relative to the size of the tusks, the pulp cavity is small, and the closure of the cavity apparently does not influence tusk mass significantly, or else the increase is offset by wear. In males this process does not occur as the increase in cavity volume continues to an age of at least 55 years.

In most elephants there is a difference in the

weight of the two tusks. As noted above, the reason for the difference is probably due to the lighter tusk being used more often for bark stripping and digging, and therefore abrading faster than the heavier tusk. This is supported in our study by the fact that the majority of 'ambidextrous' animals were in younger age classes, where abrasion may not yet have become a significant factor. In both males and females, left tusks were heavier more often than right tusks and thus, based on this interpretation, more KNP elephants were right-tusked than left-tusked. This is consistent with the findings of Bielert et al. 2017, from a data set derived from hunted elephants in 16 different African countries, and from individuals from both the savanna elephant and the forest elephant *Loxodonta cyclotis*. Their sample set was comprised of data from 683 individuals and showed that the vast majority of individuals (94.29%) showed asymmetries in tusk weight, with the left tusk also being significantly heavier than the right. Although tuskless males have been seen in the KNP (Whyte, pers. obs.) all of the tuskless elephants recorded in this sample were females. Males' tusks, being more robust than those of females, may be better able to withstand impact resulting in a lower number with missing tusks than females. The youngest tuskless animal in the sample was nine years old and the youngest that had only one tusk was seven.

In KNP, none of the tuskless animals recorded were from the same family groups, which is evidence that tusklessness in KNP is not passed genetically from mother to offspring. This contrasts with South Luangwa National Park in Zambia, where Jachmann et al. (1995) found that tusklessness appeared to run in families and that it was sex related. They suggested that a tuskless female would tend to produce tuskless daughters even if the father had tusks, but that her sons would be tuskless only if the father was tuskless himself. A further study in Addo Elephant National Park (RSA) found that very few females there have tusks. This was ascribed to the early ivory hunting in which the tusked animals were all shot, leaving only tuskless animals to breed, and eliminating the gene for tusks from the gene pool of this population (Whitehouse 2006). As indicated above, among elephants sampled in KNP, injury and breakages appeared to be the major cause of tusklessness. The condition of the alveoli in the skulls might have confirmed this, but the skulls were not available for inspection and thus genetic inheritance cannot be ruled out. Further study is required to elucidate the phenomenon of tusklessness, particularly among female elephants.

Our findings regarding tusk growth can also be interpreted in different ways. For males, Helen Mumby

(pers comm.) has suggested that apparent increase in tusk mass with age could be due to differential survival rates resulting from tusk size, i.e. that animals with larger tusks have a greater survival potential. The observed increase might not be simply from tusk growth rates derived from cross sectional population data across individuals of different ages. Whyte (2001) however, has shown that mortality rates in KNP elephants are extremely low (an average of 3.2% per year) and therefore, survival is not likely to be influenced by tusk growth parameters.

While neither Laws (1966) nor Sikes (1971) suggested a cessation of tusk growth in females, an examination of Laws' data shows that lighter tusk weights were also recorded in females in the older age classes, also beginning at about 40 years of age. This suggests that a decline in tusk weight also occurred in the western Ugandan female elephants studied by Laws. However, from observation by the authors, we suggest that regional differences might exist, especially among female elephants in East Africa whose tusks appear to be significantly larger than those in KNP. Comparisons with other regions using similar mathematical models might prove fruitful if the data existed.

The low incidence of tusklessness shows that, for both sexes, tusks must be an important tool both for use in foraging and as weapons; but the fact that tuskless animals survive shows that they are not essential for the survival of the individual. Size is clearly less important for females than for males and their tusks are probably used for foraging rather than as weapons. The cessation of growth in females' tusks at about 40 years old suggests that there may be other priority uses for dietary calcium and other elements for older female elephants. For example, to reduce the heavy demands on the female during pregnancy and lactation, these resources may be better invested in their offspring.

In males, however, tusk size must be more important. It is difficult to imagine that very large tusks would be more useful as weapons or tools than smaller ones, but it may be that larger tusks are of symbolic value in dominance skirmishes or displays. Males with larger tusks might be expected to occupy higher positions in the hierarchical structure or to be favoured as mates by females. However work in Amboseli National Park, Kenya (Moss, 1983; Poole, 1989a) suggests that the phenomenon of 'musth'

is far more important than body size in determining a male's hierarchical position and its success in mating. The condition of musth is easily recognisable to other elephants and the position in the social hierarchy of a male in musth is immediately elevated above all non-musth males. Even when two large males are simultaneously in musth, Poole (1989b) found that the factor determining dominance rank in both musth and non-musth males was body size. Tusk size is not mentioned by Moss (1983) or Poole (1989b) as a factor affecting hierarchical position. The evolutionary reason why some elephant males have large tusks is therefore still unclear, and would be an interesting subject for further research.

In KNP males, there was considerable variation in the mass of the tusks at any given age. The tusks of most males never achieve a significant size, but a young male with large tusks could almost certainly become a 'tusker' in later life. A "tusker" is a loose term which is nowhere properly defined. In KNP, a bull can become a 'tusker' when his tusks become large enough so as to become individually recognizable, regardless of their actual weight (Marais and Hadaway 2006). Hunters speak of '100 pounders' (45.5 kg), which have also become known as 'great tuskers', while Rowland Ward (2018) considers an '80 pounder' (36.4 kg) to be a 'trophy'. Such 'great tuskers' are of considerable conservation value. For hunters, in areas where elephants may be legally hunted, the current dearth of 'trophy' males, i.e. those with tusks in excess of 36.4 kg, is likely due to the fact that they are shot before their tusks grow to any substantial size. Both poaching and hunting thus promote the survival of elephants with smaller tusks, which is contrary to the interests of conservation, tourism and hunting. The concept of non-fatal "green hunting" (Douglas-Hamilton 1998), in which the hunter shoots the animal with an immobilising dart rather than with a rifle is yet to become popular (Douglas-Hamilton 1988). This would allow young males with potential to survive until such "trophy" status was achieved. Also, should large tusks be genetically inherited from the father, the selective hunting of 'trophy males' would have the effect of eliminating them from the gene pool.

Our results suggest that it would be problematic to attempt to use tusk size to determine an elephant's age. The age of an elephant, using its tusk mass and length parameters applied to the asymptotic or multiplicative equations given here, could be estimated, but given the wide variation in these parameters at any given age, estimates would be highly unreliable and therefore of little use. Application of more intensive multivariate statistical analyses to these data might be used to

Tusk Growth Characteristics in Female Elephants

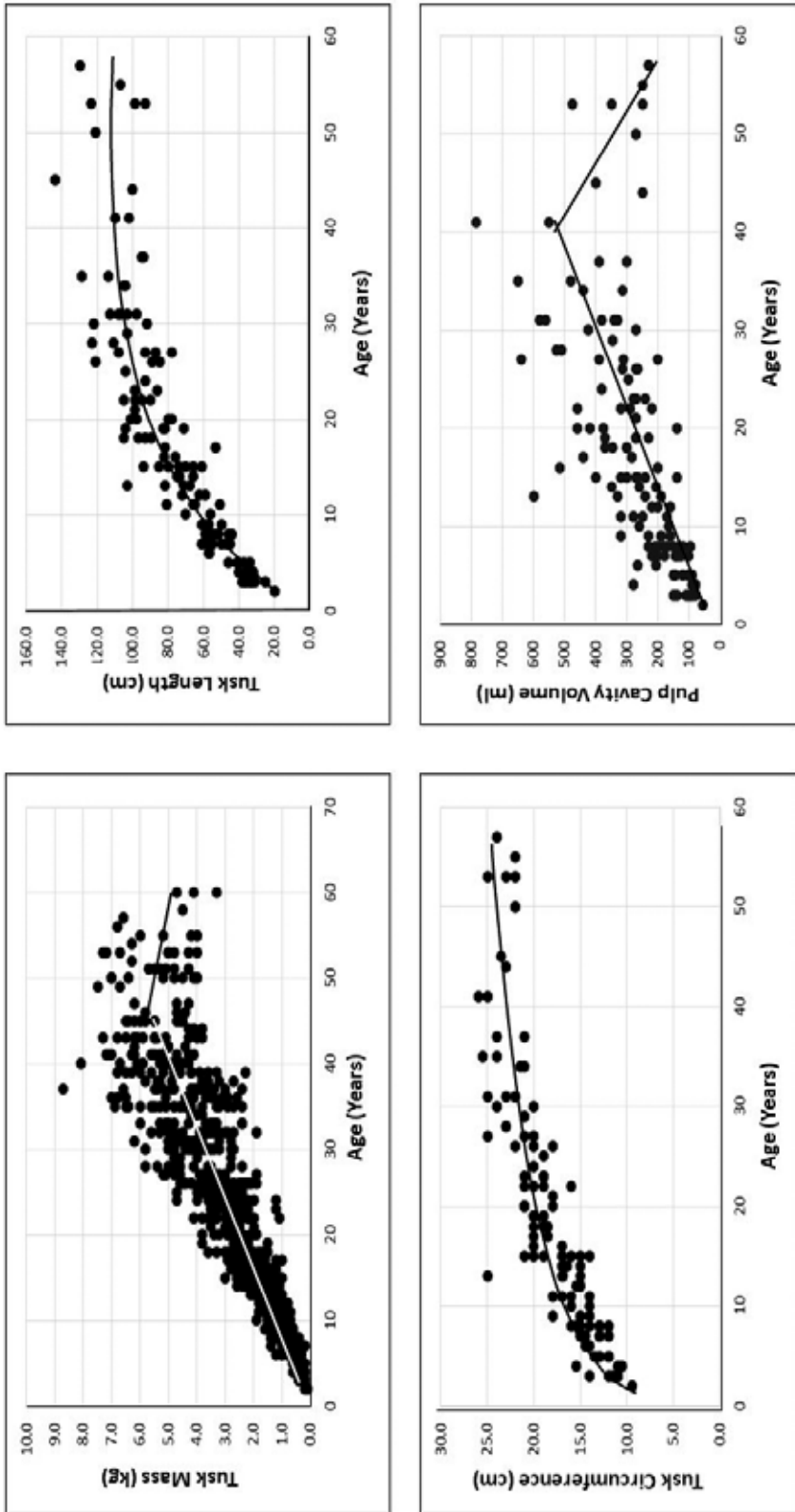


Figure 2. Characteristics of tusk growth in female elephants from the Kruger National Park.



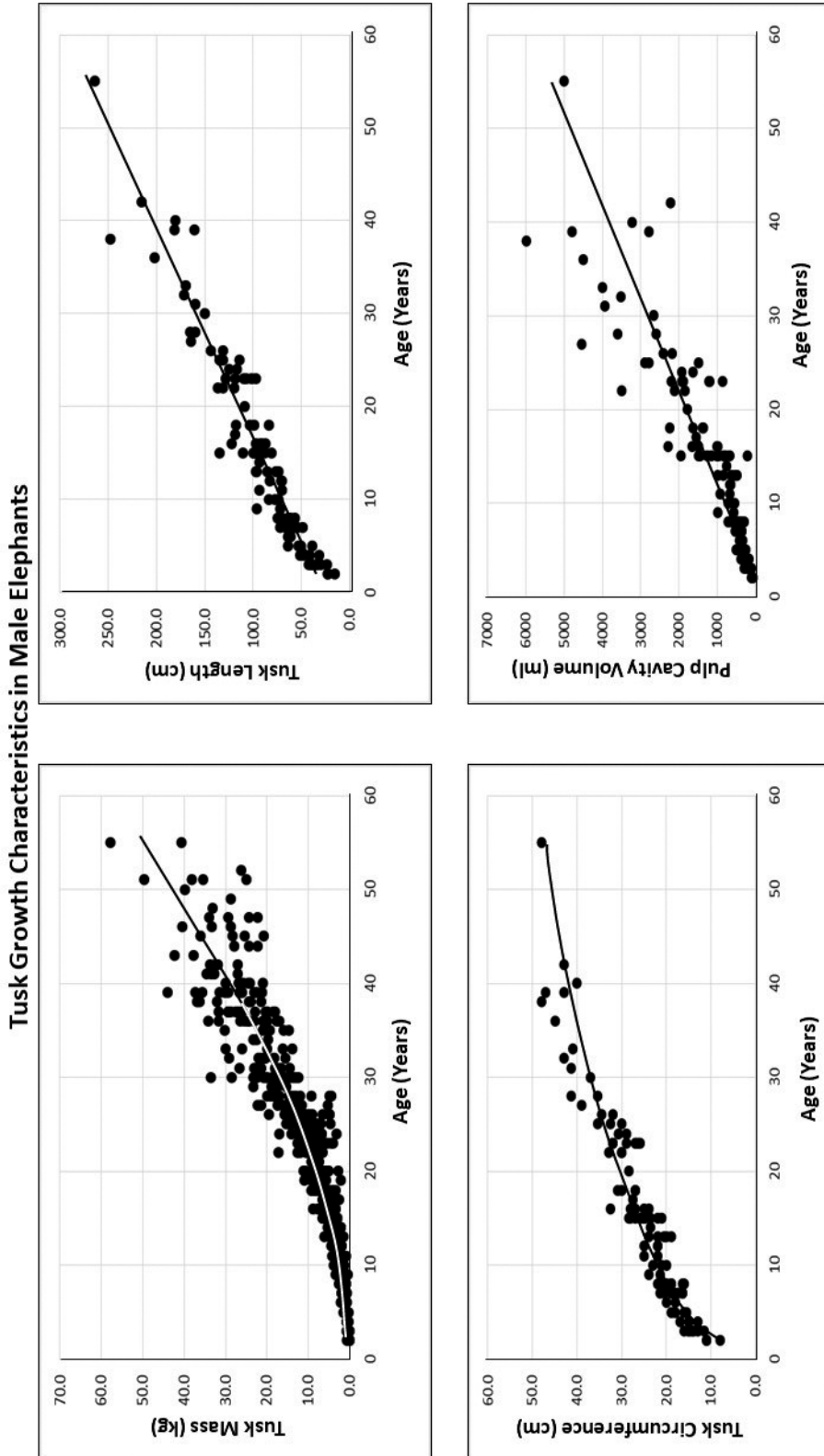


Figure 3. Characteristics of tusk growth in male elephants from the Kruger National Park.

estimate the age and sex of animals from seized ivory, or to derive population data from ivory stockpiles. However such conclusions might prove to be applicable only to KNP tusks, as populations from other regions may show other growth patterns. Indeed the evidence for differences in tusk parameters among elephants from different regions was one of the most suggestive conclusions of this study. The results will contribute to further studies investigating differences among African elephant populations and the extent to which these are genetically and/or environmentally determined.

## Acknowledgements

Particular thanks are due to Mrs. Colleen Wood for the meticulous capture of the data on computer. Mrs Wood and Mr. Obert Mathebula collected most of the data in the field. Dr. Harry Biggs and Dr. Theo Wassenaar assisted with the non-linear regression analyses. Prof. Rudi van Aarde made useful comments on an earlier draft.

## References

Bielert C, Costo N, Gallup A. 2017. Tuskedness in African elephants – an anatomical investigation of laterality. *Journal of Zoology* 304(3):1-6.

Douglas-Hamilton I. 1998. Proposal for "Green Hunting" of elephants as an alternative to lethal sport hunting. Proceedings of the African Elephant Specialist Group Meeting, Ouagadougou, February 1998. *Pachyderm* 27: Jan-June 1998

Du Toit SHC, Herbst A. 1981. The interactive computer program ST-kromme for the analysis of growth curves. *Manual for the South African Human Sciences Research Council*: 1-7 [In Afrikaans].

Elder WH. 1970. Morphometry of elephant tusks *Zoologica Africana* 5(1):143-159.

Jachmann H, Berry PSM, Imae H. 1995. Tusklessness in African elephants: a future trend. *African Journal of Ecology* 33:230-235.

Laws RM. 1966. Age criteria for the African elephant *Loxodonta africana*. *East African Wildlife Journal* 4:1-37.

Lee Thorpe JA. 1991. Where did you get that tusk? *Australian Journal of Natural History* 23:673.

Marais J, Hadaway D. 2006. Great Tuskers of Africa. Penguin Books, Johannesburg.

Moss CJ. 1983. Oestrus behaviour and female choice in the African elephant. *Behaviour* 86:167-196.

Perry JS. 1954. Some observations on growth and tusk weight in male and female African elephants. Proceedings of the Zoological Society of London 124:97-104.

Pienaar UdeV, van Wyk P, Fairall N. 1966. An aerial census of elephant and buffalo in the Kruger National Park and the implications thereof on intended management schemes. *Koedoe* 9:40-107.

Pilgrim T, Western D. 1986. Inferring sex and age of African elephants from tusk measurements. *Biological Conservation* 36:39-52.

Poole JH. 1989a. Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour* 37:842-849.

Poole JH. 1989b. Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour* 37:140-152

Raubenheimer EJ, Dauth J, Dreyer MJ, Smith PD & Turner ML. 1990. Structure and composition of ivory of the African elephant (*Loxodonta africana*). *South African Journal of Science* 86:192-193.

Raubenheimer EJ, Dauth J, Van Heerden WFP, Smith PD, Dreyer MJ, De Vos V. 1991. Hypoplasia of elephant tusks: a comparative biochemical investigation *Journal of Dental Research* 70(4):849.

Raubenheimer EJ, Osborn J, Dauth J, van Niekerk J, Lemmer LB, de Vos V. 1989. Structure of the tusk of the African elephant *Loxodonta Africana*. *Journal of Dental Research* 68(4):730.

Raubenheimer EJ, van Heerden WFP, van Niekerk PJ, de Vos V, Turner MJ. 1995. Morphology of the deciduous tusk (tush) of the African elephant (*Loxodonta africana*). *Archives of Oral Biology* 40(6):571-576.

Rowland Ward. 2018. Rowland Ward's Records of Big Game. <https://rowlandward.com/>

Smuts GL, Anderson JL, Austin JC. 1988. Age determination in the African lion (*Panthera leo*). *Journal of Zoology*, London 185:115-146.

Sikes SK. 1971. The natural history of the African elephant. Weidenfeld and Nicholson, London.

van Wyk P, Fairall N. 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* 12:66-75.

Whitehouse AM. 2006. Tusklessness in the elephant population of the Addo Elephant National Park, South Africa. *Journal of Zoology* 257(2):249-254.

Whyte IJ. 2001. Conservation management of the Kruger National Park elephant population. PhD. Thesis. University of Pretoria, Pretoria.