Further observations on savannah elephant tusks

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Abstract

The paper analyses weights of 2,425 tusk pairs, and lengths of 398 pairs obtained between 1965 and 1969 from two East African savannah elephant populations, one in Uganda, the other in eastern Kenya and north-eastern Tanzania. They are presented as averages in five-year age cohorts. Separately, length, weight and gender showed no significant differences between the use of the right and left tusks. If neural lateralization exists in elephants, it is concealed by the dynamics of tusk growth and wear, which are described. The fact that average asymptotes at age are only 31% (female) and 38% (male) of the theoretical asymptotes is explained by weathering and wear. Contrary to expectations that single tusks, having to do the work of two, would be shorter than the pair average, they are not, but stay within pair length parameters. Evidence is presented that declining tusk growth occurs in both sexes with advanced age. The longer-tusk pairs have a tight curvilinear relationship to average shoulder height, rising evenly from 24% (females) and 26% (males) under 6.5 years to 58% and 76% respectively in the oldest age classes. That is, they relate to an elephant's height.

Résumé

Dans cet article, nous analysons le poids de 2 425 paires de défenses et la longueur de 398 paires obtenues entre 1965 et 1969 sur deux populations d'éléphants de savane d'Afrique : l'une en Ouganda, la deuxième dans l'est du Kenya et le nord-est de la Tanzanie. Les données sont présentées sous forme de moyennes par cohortes d'âges de cinq ans. Pris séparément, la longueur et le poids des défenses ainsi que le sexe de l'animal ne montrent pas de différences significatives entre l'utilisation des défenses droite et gauche. Si la latéralisation cérébrale existe chez les éléphants, elle est cachée par les dynamiques de croissance et d'usure des défenses, qui sont décrites. Le fait que les asymptotes moyennes à l'âge ne représentent que 31 % (chez les femelles) et 38 % (chez les mâles) des asymptotes théoriques s'explique par l'altération et l'usure. Contrairement à ce que l'on pourrait penser, une défense unique, devant effectuer le travail pour deux, n'est pas plus courte que la moyenne des paires, mais reste dans les paramètres de longueur de la paire. Il est prouvé que la baisse de croissance des défenses se produit chez les deux sexes à partir d'un certain âge. Les paires de défenses les plus longues ont une relation curvilinéaire étroite avec la hauteur moyenne des épaules, passant uniformément de 24 % (femelles) et 26 % (mâles) en dessous de 6,5 ans à, respectivement, 58 % et 76 % dans les classes d'âge les plus élevées. En somme, leur longueur est relative à la hauteur de l'animal.

Introduction

Given the elephant's size and longevity, much previous research has, perforce, had only small samples and individual cases to deal with. Here I had the advantage of large samples. Larramendi (2023) comprehensively summarizes knowledge of proboscidean tusks, extinct and extant. The field has been researched with a focus on taxonomy, particularly by Osborn (1936, 1942). What follows extends and/or qualifies previous records of savannah elephant tusk morphology by Elder (1970) and Raubenheimer et al. (1989).

In elephants, all three components of mammalian teeth – cementum, enamel and dentine – are present.

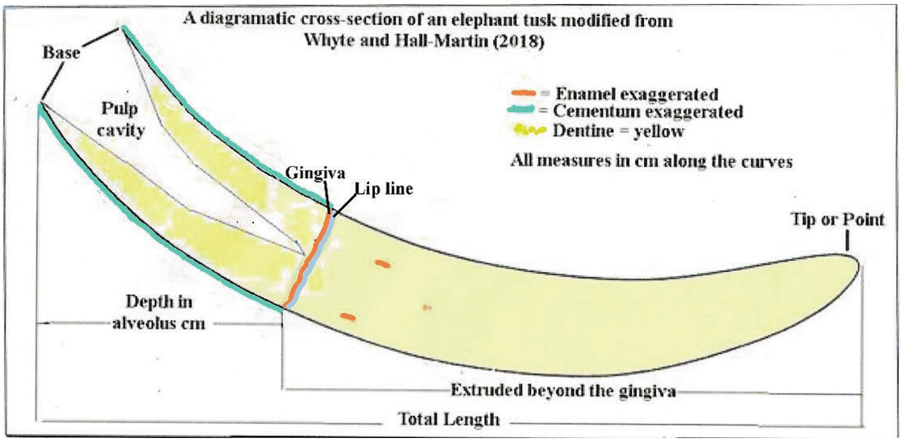


Figure 1. Characteristic features of a tusk (adapted from Whyte and Hall-Martin 2018).

Figure 2. Growth rings are obvious in the alveolar sections of all tusks. They occur like tree rings throughout their entire dentine body but are only visible in lateral and longitudinal cross-sections.

Cementum plays its internal role as a thin sheath that via the periodontal ligament bonds the tusk to the surrounding alveolar bone. Enamel occurs variably within proboscidean taxa as a very thin lateral layer as the tusk emerges from the alveolus but is only known as a cap in juvenile tusk tips in extant elephants (Larramendi 2023). In the savannah elephant tusk, the enamel is only sustained as a cap over the erupting tusk bud, which is usually abraded away when less than 30 cm of the tusk is beyond the lip fold (pers. obs. 1960s; Whyte pers. comm. 2018). Thereafter, if present at all, it is very thinly and unevenly distributed along the external elephant tusk shaft beyond the gingiva, tending to persist in longitudinal grooves deep enough to protect it from wear (pers. obs. 1960s), but seemingly serving no structural role. As an aside, Nasoon (2020) records similar enamel caps on emergent walrus (*Odobenus rosmarus*) tusks, and Berkovitz (2016) noted them on narwhal (*Monodon monoceros*) tusks that are also composed of dentine. In both species, and as observed on East African elephant tusks by myself and by Whyte in tusks from the Kruger National Park, these enamel caps are soon lost and may provide the emergent tusks some protection while they are still too small to withstand unprotected use.

In the tusk of the savannah elephant, dentine (ivory) has replaced the functional role of enamel. However, unlike enamel, which is hard, inflexible and brittle, dentine is relatively soft, slightly flexible (Kingdon 1979), and easily worn down. Ivory flexibility is obvious when reduced to a flat blade like a bendable paper knife, but this is limited by the circular cross-section of the entire tusk. As observed by Raubenheimer et al. (1989), and noted in Larramendi (2023), what tusks lose through abrasion is exceeded by the constant growth recorded by Laws (1966), which allows size to increase throughout life.

Parker (2024) describes symmetry in tusk pairs in the metrics of weight, length and circumference related to the ages of elephants. Here, that study is extended, to address the difference between measured asymptotes of tusk weight and length (females: 160 cm; males: 250 cm) (Parker 1979) and Laws' (1970) theoretical asymptotes (female: 510 cm; males: 660 cm) calculated from dental growth rings (vide Laws 1952), such as those shown in Fig. 2.

This paper examines evidence of whether savannah elephants are neurally predisposed to use their tusks in the sense that people are right-handed/left-handed or ambidextrous. It tests the hypothesis that single tusks are shorter than those in pairs due to doing the work of two. It discusses observations on tusk growth and how dentine is lost through abrasion and breakage. Finally, it explains the paradox of how tusk sizes so closely correlate with age (Laws 1966), while being subject to many random, stochastic influences (breakage and accidents) in long lives, that might reasonably be expected to disrupt close correlation.

Materials and methods

This paper is based on hard data acquired from five clans culled from two savannah elephant populations: one in west-central Uganda, the other in the Nyika biome, comprising Kenya's and north-easternmost Tanzania's coastal hinterland, as described in Laws et al. (1975) and Parker and McCullagh (2021) (Table 1). However, it is also informed by personal experience accumulated between 1956 and 2000, first as a game warden, and then while documenting the ivory trade and handling many thousands of tusks in 11 African countries, Britain, Belgium, Germany, India and Hong Kong (Parker 1979).

For this study and given both the small differences between them (Parker 2024) and to minimise the possible flaws in the Laws (1966) aging system (Parker 2023), the five-clan data have been combined and pooled into five-year age cohorts. Where useful, however, the two Uganda clans are referred to as Murchison North and Murchison South, located to the north and south of the Victoria Nile, respectively, and the three in the Nyika biome as Tsavo Koito, Mkomazi East and Mkomazi Central.

In some culls, age was ascribed without decimal points. In others, ages were recorded variably: some neonates were recorded as 0, while ages of others, particularly calves but also few older animals, were estimated to one decimal point. Here, across all clans, ages were standardized into year classes 0.5, 1.5, 2.5 .... where 0.5 = 0–0.9, 1.5 = 1.0–1.9, etc.

The study does not include data on milk tusks (tushes) or pre-emergent permanent tusks before they show through the gingivae as they were not collected. Tusk pair data recorded from all elephants included whether right or left, lengths (to 0.5 cm), weights (to 0.25 kg), sex, age, and shoulder height (cm). Elephants less than 6 years of age, whose tusk pairs may not have fully erupted and usually show few signs of abrasion by use, were examined separately for evidence of a congenital difference between the right and left.

Table 1. The five study populations, showing regions, sampling areas, population designations (clan), sampling locations (coordinates), sample sizes, and date ranges when sampling took place. NP = National Park

Region	Sampling area	Clan	Coordinates	Sample size	Dates
Murchison	Murchison Falls NP, Uganda	Murchison North	2°24'N, 31°42'E	1,197	Mar 1965–Jun 1967
		Murchison South	2°10'N, 31°50'E	798	Nov 1965–May 1967
Nyika	Tsavo NP, Kenya	Tsavo Koito	3°00'S, 38°42'E	298	Aug 1966
	Mkomazi NP, Tanzania	Mkomazi East	4°22'S, 38°35'E	299	Mar–Apr 1968
		Mkomazi Central	4°9'S, 38°14'E	295	Aug–Sept 1969

Results

Paired tusk length data were obtained from 189 females and 177 males, all over 6.5 years of age. A paired *t*-test for the null hypothesis (Quinn and Keough 2002) found no significant difference between right and left tusks (females: p = 0.87; males: p = 0.84) (Table 2; Fig. 3 a and b).

Overall differences expressed as proportions of the average pair's longer tusk did not exceed 3.1% in females and 1.0% in males; in both cases, these maxima were in the oldest class. This closeness notwithstanding, as would be expected from cumulative, stochastic wear and breakage over time, the proportion of equal-length pairs was greatest in the youngest cohort (females: 52.2%; males 38.7%), becoming slightly less equal with increasing age to midlife. The ratio rose again with increasing age (Fig. 4), the most likely reason being an artefact from inadequate older elephant data.

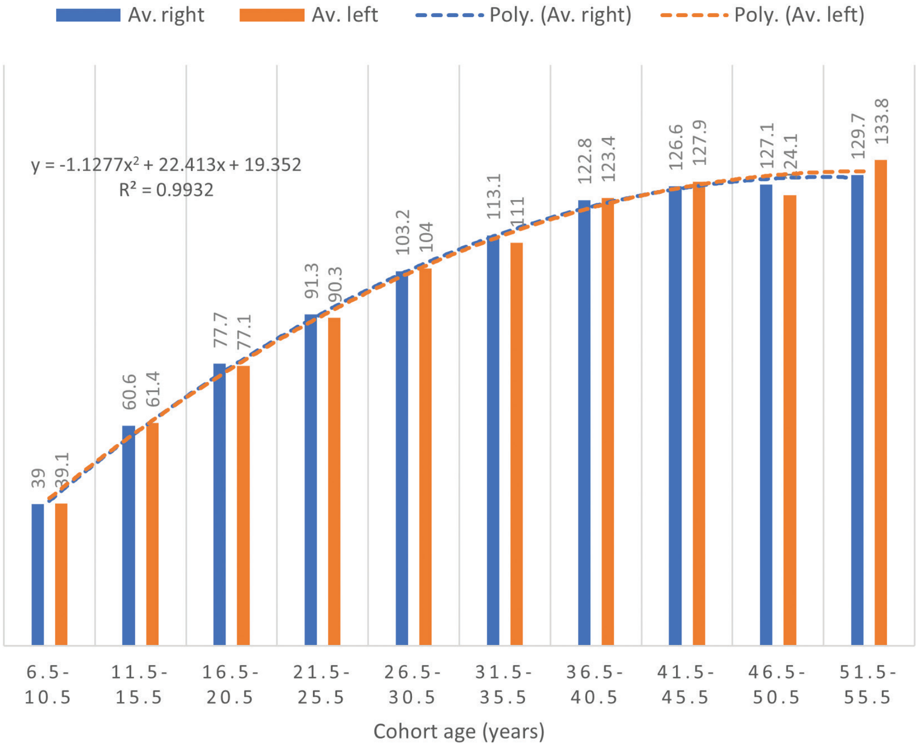
Paired tusk weight data were available from 1,304 females and 1,021 males, all over the age of 6.5 years. A paired *t*-test for the null hypothesis (Quinn and Keough 2002) found no significant difference in weight between right and left tusks (females: p = 0.83; males p = 0.504) (Table 3; Fig. 5).

The information in Table 3 above is represented

Table 2. Tusk pair lengths (cm) from 212 female and 186 male elephants between the ages of 6.5 and 55.5 years, as averages of five-year cohorts.

Age cohort	No. in cohort	Right tusk		Left tusk	
		Mean	SD	Mean	SD
Females					
0–5.5	23	39.0	2.54	39.1	2.57
6.5–10.5	31	60.6	2.66	61.4	3.50
11.5–15.5	31	77.7	2.79	77.1	2.00
16.5–20.5	21	91.3	3.53	90.3	3.22
21.5–25.5	35	103.2	3.29	104	3.27
26.5–30.5	19	113.1	3.30	111	3.01
31.5–35.5	8	122.8	3.20	123.4	3.81
36.5–40.5	10	126.6	2.95	127.9	2.48
41.5–45.5	5	127.1	1.89	124.1	2.98
46.5–50.5	20	140.7	3.54	137.1	3.34
51.5–55.5	6	151.8	2.52	154	4.12
56.5–60.5	3	143.0	3.26	138.8	3.81
Totals	**212**				
Males					
0–5.5	31	43.4	2.90	43.5	2.87
6.5–10.5	52	74.6	3.45	75.0	3.42
11.5–15.5	31	103.3	3.00	103.1	3.10
16.5–20.5	28	122.6	3.17	122.4	3.31
21.5–25.5	12	137.9	3.35	136.9	3.53
26.5–30.5	18	155.8	3,55	154.3	3.72
31.5–35.5	5	181.8	0.26	183.6	1.16
36.5–40.5	1	230.0	15.2	228.0	15.10
41.5–45.5	6	186.6	4.92	176.9	4.28
46.5–50.5	2	224.0	0.81	248.0	0.81
Totals	**186**				

(a) Average length of female tusk pairs



(b) Average length of male tusk pairs

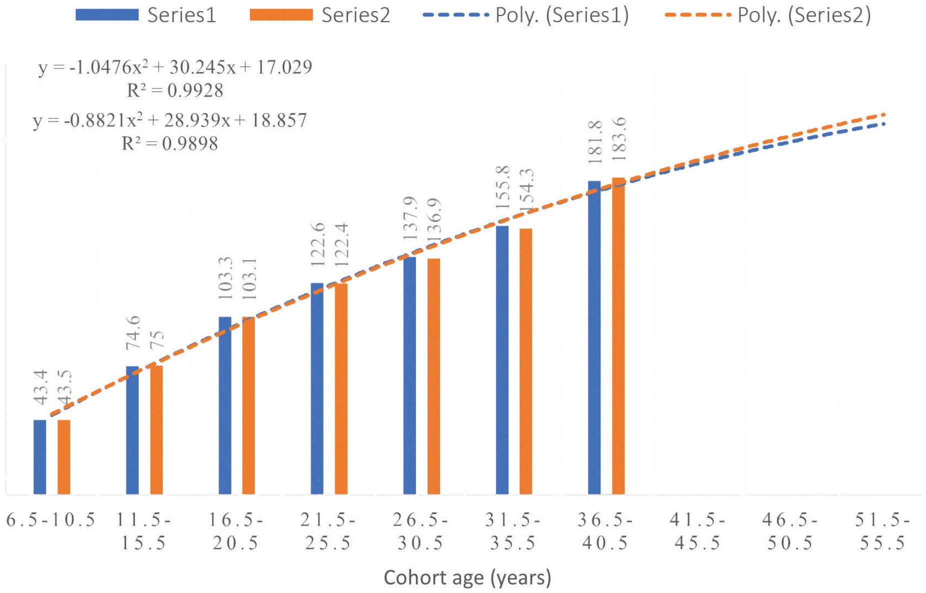


Figure 3. Average left and right tusk lengths for (a) female (n = 189) and (b) male (n = 177) elephants. Cohort ages are averages, i.e. 8.5 = 6.5–10.5, 13.5 = 11.5–15.5, etc. Bar labels indicate mean values for each age cohort. Dashed lines show curvilinear fits based on second-order polynomial regressions.

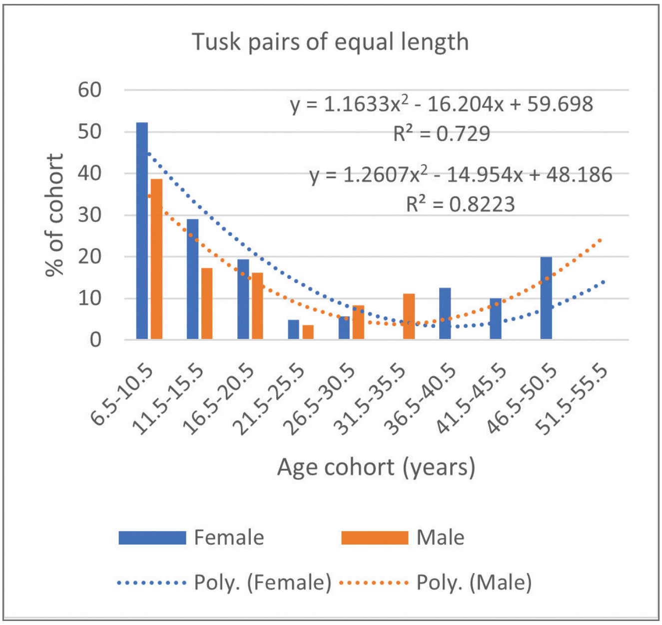


Figure 4. Proportion of tusk pairs of equal lengths in female (n = 189) and male (n = 177) elephants. Cohort ages are averages, i.e. 8.5 = 6.5–10.5, 13.5 = 11.5–15.5, etc. Dashed lines show curvilinear fits based on second-order polynomial regressions.

graphically in Fig. 5 a and b, below.

Proportions of pairs of tusks of equal weight in each age cohort follow similar trajectories to those for length pairs, being greatest early in life, declining to midlife, and then levelling out (Fig. 6).

Bearing in mind that tusk lengths and weights are predictive of one another (Parker 2024), the results for the larger weight sample makes the upswing in the proportion of equal length tusks in later life (Fig. 4) all the more likely to be an artifact of too few data.

When presented as averages in five-year cohorts, neither in length nor weight do tusk pairs display any bias to either right or left, confirming that finding in Parker (2024). To address the possibility that tusk metrics are nevertheless influenced congenitally, the lengths were examined of 69 tusk pairs of elephants under 5.5 years old, before tusks can be much worn in use and when most still have enamel caps. Table 4 presents average lengths (cm) from 69 tusk pairs (31 female and 38 male).

The data in Table 4 suggests some level of inequality. With 31 females, mean right and left tusk lengths were the same (38) cm (paired *t*-test =1.00). In 38 males, the mean tusks of the right and left tusks were 41.4 and 41.6 cm, respectively (paired t = P 0.28). However, pairs of exactly equal length were 39.1% of the sample, while the remaining 60.9% were very slightly unequal. Statistically, therefore, though there was no significant length difference between right and left tusks, within each sample, more emergent tusks than not are congenitally slightly different. While not statistically significant, given the measurements made, this leaves the question of congenital influence on tusk metrics open. Suffice it to say, as far as this study goes, there is no evidence of lateralization in emergent tusks, but with 60% unequal, not all tusk pairs start as mirror images of one another and some length differences may be congenital.

The relationship of lengths to weights, in samples of 561 tusk pairs (272 females, 289 males) is given in Table 5. The longer tusk was also heavier in 80.0% of females and 80.6% of males. The right tusk was longer, but the shorter left tusk heavier in 5.6% of females and 4.5% of males. The left tusk was longer, but the shorter right tusk heavier in 4.8% of females and 6.6% of males. The right and left tusks were equal in both length and weight in 9.6% of females and 8.3% of males.

Differing gender tusk shapes (*in alveolum* before any wear can have influenced them) are illustrated in

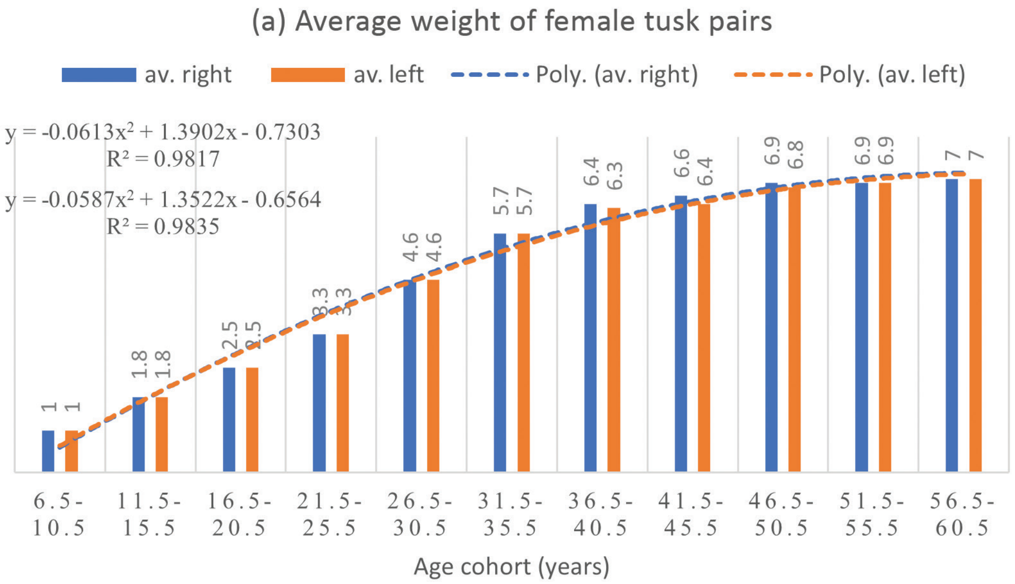
Table 3. Comparison of average weights (kg) of the summed cohort between the right and left tusks in samples of 1,304 female and 1,021 male tusk pairs, presented in five-year cohorts from 6.5 to 55.5 years.

Age cohort	No. in cohort	Right tusk		Left tusk	
		Mean	SD	Mean	SD
Females					
0–5.5	122	0.39	0.44	0.39	0.44
6.5–10.5	219	1.00	0.53	1.00	0.53
11.5–15.5	165	1.78	0.57	1.79	0.64
16.5–20.5	184	2.51	0.68	2.50	0.66
21.5–25.5	190	3.32	0.77	3.32	0.77
26.5–30.5	174	4.61	0.92	4.62	0.93
31.5–35.5	102	5.54	0.94	5.67	0.99
36.5–40.5	94	6.34	1.08	6.35	1.08
41.5–45.5	50	6.73	1.08	6.42	1.01
46.5–50.5	53	7.55	1.06	7.49	1.06
51.5–55.5	39	6.96	1.19	6.87	1.13
56.5–60.5	12	6.97	1.11	6.97	1.04
Totals	**1,404**	**3.35**	**0.75**	**3.35**	**0.75**
Males					
0–5.5	160	0.59	0.52	0.60	0.52
6.5–10.5	263	2.03	0.79	2.06	0.75
11.5–15.5	188	4.02	0.90	4.01	0.90
16.5–20.5	152	9.57	1.35	9.47	1.34
21.5–25.5	19	14.25	1.69	14.20	1.72
26.5–30.5	47	18.67	2.35	19.00	1.61
31.5–35.5	25	25.91	2.49	26.00	2.38
36.5–40.5	17	30.74	2.65	29.41	2.57
41.5–45.5	8	39.61	2.53	38.16	2.57
46.5–50.5	2	39.30	2.72	38.6	2.90
Totals	**1,021**	**39.3**	**1.14**	**38.6**	**1.12**

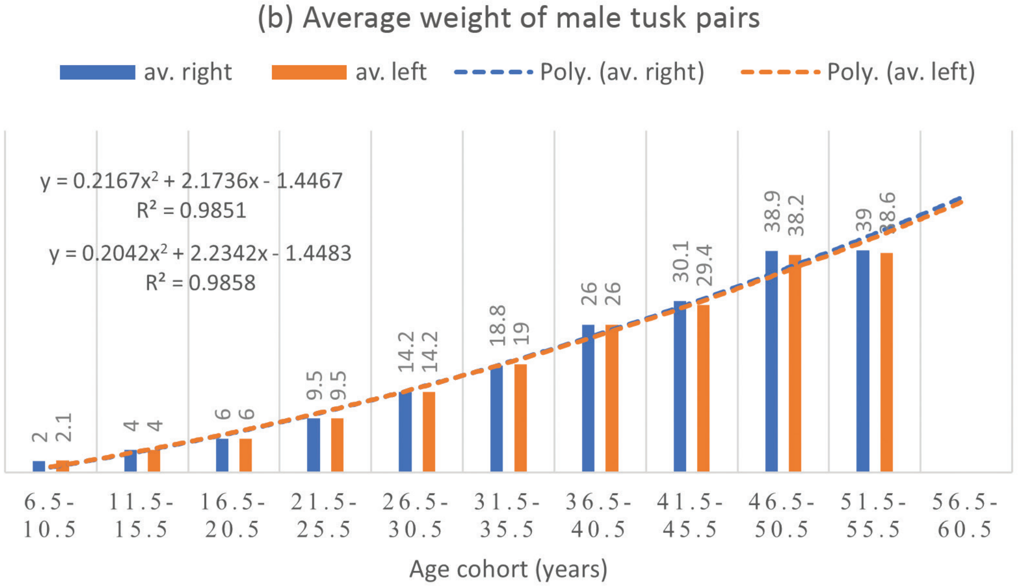
Table 6 and Figure 7 where, as an index of taper (cone shape), the difference between the tusk base and lip diameters is given as a percentage of the former and related to the elephant's age. From these data, it is apparent that males' tusks retain a conical form until around the mid-20s, after which the slope decreases and in old age has reversed. Female tusks are more cylindrical until the mid-30s, after which, as with males, the base diameter decreases. In both sexes, this pattern suggests slower growth in late age.

The difference in typical tusk shape between the sexes (females cylindrical, male conical) shown in Fig. 7 is illustrated visually in Fig. 8.

That female and immature elephants associate as family units under the leadership of a matriarch was noted by Laws et al. (1975) and described in detail by Moss and Poole (1983). Their findings are further supported by photographs of the tusks of two such families shown in Figure 9. Those on the left were registered by Game Management Uganda as herds GMU 30 and those on the right as GMU 32. In each, the oldest female's (assumed matriarch's) right and left tusks are at the centre opposite one another and



(a) Average weight of female tusk pairs



(b) Average weight of male tusk pairs

Figure 5. Average left and right tusk weights for (a) female (n = 189) and (b) male (n = 177) elephants. Cohort ages are averages, i.e. 8.5 = 6.5–10.5, 13.5 = 11.5–15.5, etc. Bar labels indicate mean values for each age cohort. Dashed lines show curvilinear fits based on second-order polynomial regressions.

the rest of the herd's tusks are laid in descending age order outwards with the youngest pair at the outer edges. Both herds reflect their individual matriarch's distinctly different and presumably inherited tusk curvature in one plane.

Table 7 and Fig. 10 use the close genetic links within elephant families to estimate tusk growth and wear from use over an individual lifespan. They present data from 1966 on the six females of different ages of herd GMU 32, showing for each animal the measured tusk length and potential tusk length based on Laws' (1970) estimate of annual female tusk

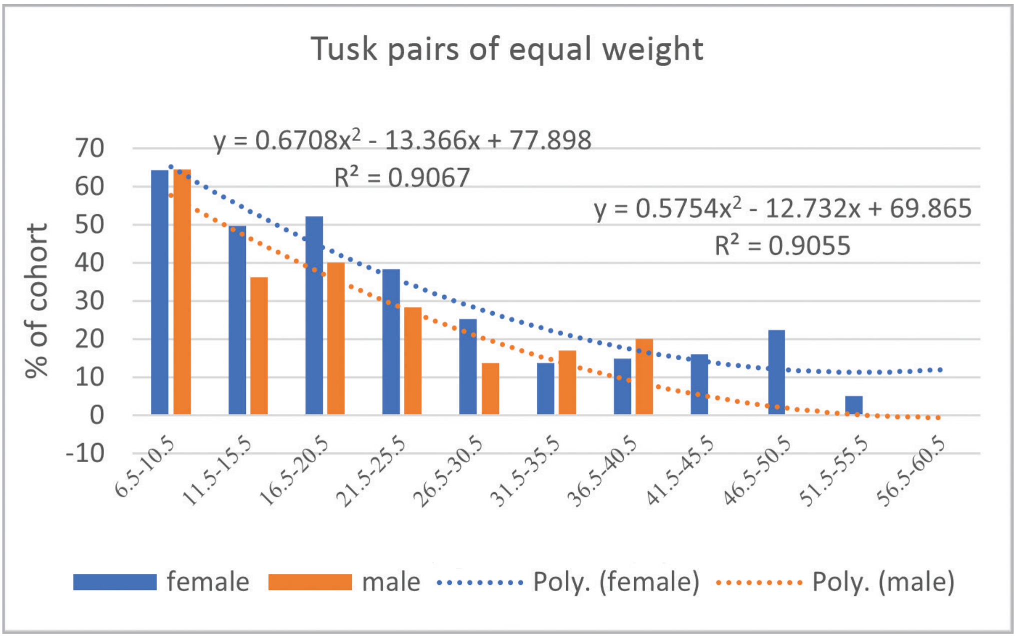


Figure 6. Proportion of tusk pairs of equal weights in female (n = 189) and male (n = 177) elephants. Cohort ages are averages, i.e. 8.5 = 6.5–10.5, 13.5 = 11.5–15.5, etc. Dashed lines show curvilinear fits based on second-order polynomial regressions.

Table 4. Comparison of the lengths of tusks (cm) in 69 pairs of tusks (31 female and 38 male) from elephants aged 5.5 years or less.

Sex	No.	Unequal (%)	Equal (%)
Female	31	58.1	41.9
Male	38	63.3	36.8
Combined	**69**	**60.9**	**39.1**

Table 5. Lengths of tusk to their weights for females (n =272) and males (n = 289) as a percentage of each sample.

Sex	Longer tusk heavier	Right tusk longer, left heavier	Left tusk longer, right heavier	Pairs with equal length and weight	Totals
F	80.0	5.6	4.8	9.6	100.0
M	80.6	4.5	6.6	8.3	100.0

length growth of 8.5 cm. The potential lengths of the tusks are greater than the actual lengths, and the differences are presumed indices of loss.

Regressions fitted for the measured tusks at age were $y = 25.171x + 4.7333$, $R^2 = 0.9401$, and for potential length were $y = 6.0714^3 - 58.1354x^2 + 227.51x - 161.67$, $R^2 = 0.9963$. Matching data for males are not shown, as there were too few male tusks available for statistical analysis.

The expectation that a single tusk would have twice the work of those in pairs and suffer twice the wear would be shorter was tested. In a sample of 304 female elephants, 11 were single-tusked, distributed between the ages of 4 and 49 years. Samples of 10 same-age two-tusked animals for each of them were not available so their lengths were contrasted with the average tusk lengths of the 10 closest age pairs to each case. The data are given in Table 8 and Figure 11. Linear regressions with equations and coefficients of determination (nearest age pairs $R^2 = 0.945$, single tusks $R^2 = 0.771$) indicate that single tusks fall within the same scatter as tusks in pairs and are not shorter despite doing the work of two. In a sample of 274 male tusk lengths, only three were unilaterally tuskless. These were too few for worthwhile statistical analysis, but two were respectively 13% and 8.6% longer and one was 6.3% shorter than the average of their 10 closest pairs, providing no ground for assuming that a greater workload produces a shorter tusk.

Table 6. Gender differences in tusk shape, showing tusk weights, diameters (mm) of the tusk base and at the lip, the difference (mm) and difference as a percentage of the base diameter. Negative values in bold red type indicate the base diameter was less than the lip diameter. ID numbers were assigned by Game Management Uganda (GMU).

ID	Age (year)s	Tusk weight (kg)	Diameter (mm)		Difference (base–lip)	
			Base	Lip	mm	%
			Females			
1585	8	1.1	20	21	**-1**	**-5.0**
1487	9	1.1	42	45	**-3**	**-7.0**
1557	10	0.9	22	23	**-1**	**-4.5**
1507	17	1.8	32	32	0	0
1589	22	3.2	26	26	0	0
1587	23	3.6	28	28	0	0
1595	25	5.0	28	28	0	0
1502	26	2.7	26	27	**-1**	**-3.8**
1572	39	5.2	25	27	**-2**	**-8.0**
1554	47	10.4	32	33	**-1**	**-3.1**
1513	52	8.2	36	39	**-3**	**-8.3**
1515	52	6.3	30	32	**-2**	**-6.7**
1501	53	7.0	35	35	0	0
1561	53	10.4	30	30	0	0
1514	55	6.5	34	38	**-4**	**-11.8**
1484	59	9.1	30	35	**-5**	**-16.7**
			Males			
1556	5	0.9	32	28	4	12.5
1557	5	0.9	31	27	4	12.9
1572	6	1.6	33	30	3	9.1
1569	9	1.8	31	28	3	9.7
1555	10	2.7	41	37	4	9.8
1593	11	3.6	37	34	3	8.1
1440	14	5.7	44	39	5	11.4
1562	15	5.0	46	42	4	8.7
1410	17	4.1	47	40	7	14.9
1468	17	48	30	27	3	10.0
1429	21	9.7	35	30	5	14.3
1500	21	6.6	41	38	3	7.3
1416	24	7.7	50	45	5	10.0
1445	24	9.1	55	49	6	10.9
1432	26	8.6	45	44	1	2.2
1434	31	19.3	37	33	4	10.8
1407	36	24.5	40	40	0	0
1443	38	32.4	45	44	1	2.2
1466	40	43.9	36	35	1	2.8
1444	45	28.3	45	46	**-1**	**-2.2**
1546	49	66.6	30	31	**-1**	**-3.3**
1546	49	62.1	40	40	0	0

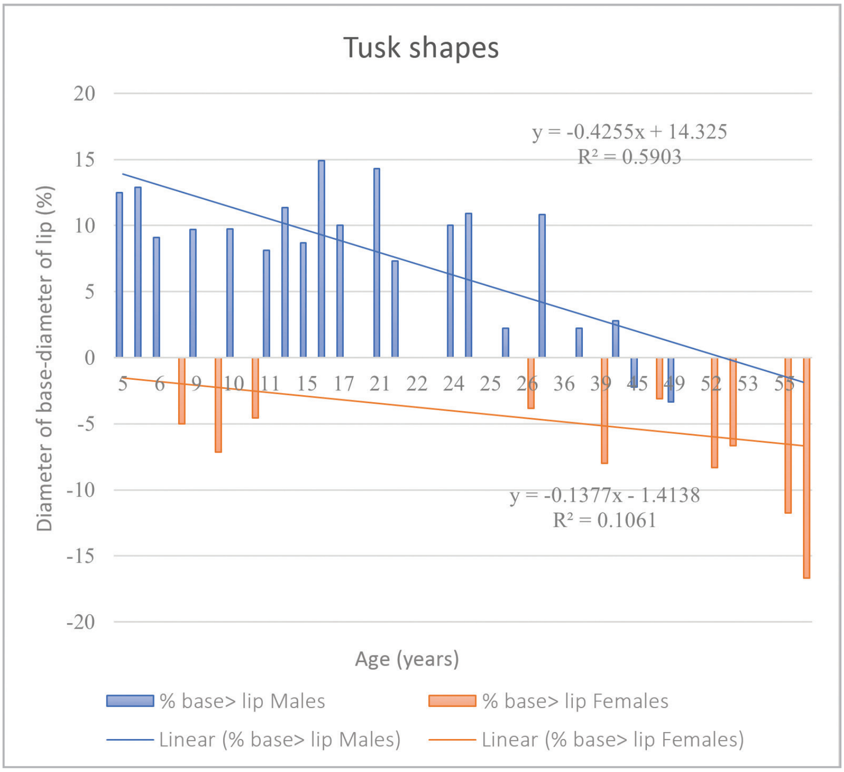


Figure 7. Tusk shape for females (n = 16) and males (n = 22) shown as the difference between diameter at the tusk base and at the lip. Positive values indicate a tapered shape where the tusk base diameter is greater than the diameter at the lip. Solid lines show linear regressions of tusk shape related to age.

Figure 8. The alveolar sections of (left) a cylindrical female tusk and (right) a tapered male tusk.

That closeness of length and weight between tusk pairs, the close relationship between tusk size and age, and the finding that single tusks were not shorter than tusks in pairs indicated that tusk length variations were responses to another driver. As body size is known to be correlated to age (Laws et al. 1975), possibly size was that driver. As shoulder heights of culled elephants were available, the relationship between this variable and the longer tusk of a pair was examined. Table 9 and Fig. 12 present the average of the longer tusks and the average of all shoulder heights at age in each five-year cohort for 289 females and 269 males.

From the youngest age class (<0–5.5) to the oldest class (56.5–60.5), the shoulder heights and tusk lengths of females have curves rising towards a maximum (Fig. 12A), which closely fit polynomial regressions (coefficients of determination, R^2 = to approximately 0.99; Quinn and Keough 2002). The ratio of tusk length to shoulder height curve is nearly linear ($R^2 = 0.99$). For males, shoulder heights and tusk lengths have similar curves to those of females, and fit well with polynomial regressions (Fig. 12B), but were more variable (R^2 varied from 0.95 to 0.98). The ratio of tusk length to shoulder height for males was also nearly linear ($R^2 = 0.89$). Using these data for females in the twelve age classes, it was found that the average length of the longer tusk length (y) can be accurately predicted from the average shoulder height

Figure 9. Examples of two herds from the same clan (Murchison South): (left) herd GMU 30 whose tusks are heavily curved, and (right) herd GMU 32 whose tusks are relatively straight.

Table 7. Measured and potential lengths of tusk of six females of herd GMU 32, showing their age in 1966, their year of birth, years between births, the matriarch's age at the time of the other elephants' births, the measured length of the longest tusk of each individual (cm), its potential length at the same age using Laws' (1970) formula, the difference between actual and potential lengths, showing estimated loss through wear, in centimetres and as a percentage of the measured length. ID numbers were assigned by Game Management Uganda (GMU).

ID	Age (years) in 1966	Year of birth	Years between births	Matriarch (235)'s age at birth	Longest measured tusk (cm)	Potential length (cm)	Loss through wear (cm)	Loss through wear (%)
235	50	1916			155	425	270	174
239	32	1934	18	18	127	272	145	114
231	26	1940	6	24	104	221	117	113
229	18	1948	8	32	81	153	72	89
228	13	1953	5	27	76	110.5	34.5	45
233	2	1964	3	48	14	(Emergent)	0	0

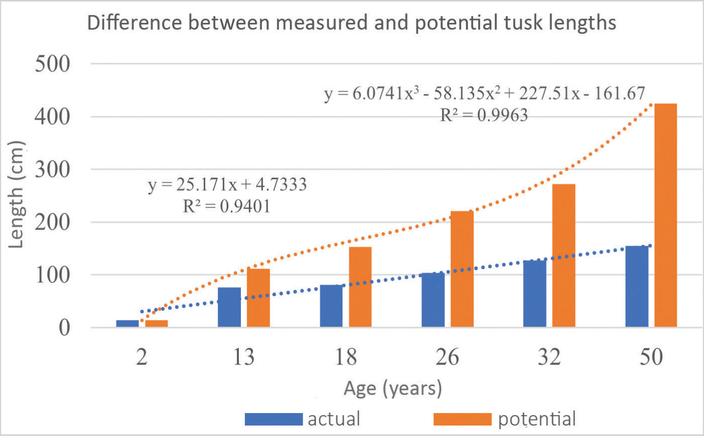


Figure 10. Actual and potential lengths of tusks for females of different ages in herd GMU 32; as an indication of tusk loss through wear. Potential lengths are estimated based on average growth of 8.5 cm a year as given in Laws (1970). Dotted lines show fits based linear (measured length) and third order polynomial (potential length) regressions.

Table 8. The tusk lengths in cm of eleven single-tusked female elephants compared to the average tusk lengths of the ten pairs closest to them in age.

Age (year class)	Tusk length (cm)	
	Paired tusks	Single tusk
4.5	42.4	42.0
7.5	54.4	44.5
8.5	63.7	51.0
13.5	81.6	81.5
18.5	86.0	51.0
18.5	88.2	94.0
20.5	84.8	107.0
22.5	98.9	67.5
30.5	120.7	128.5
43.5	127.2	174.0
49.5	147.3	132.0

(x) by the exponential growth equation $y = y_0 + ab^x$, which is best fit as $y = 22.14 + 0.7096 \times 1.0204^x$ ($r^2 = 0.99$, $p < 0.001$) (Quinn and Keough 2002). For male data in 10 age classes (with no data for the oldest two cohorts), the longest average length of the tusk was also accurately predicted from average shoulder height by the exponential growth curve, $y = -180.8 + 125.1 \times 1.0036^x$ ($r^2 = 0.92$, $p < 0.001$). Thus, the average size of female and male elephants, as measured by average shoulder height, provides a template for the average longest tusk length.

Discussion

Lateralization

In elephants <5.5 years old (69 pairs), when their enamel caps may prevent dentine erosion, some 60.9% of erupting tusk pairs were unequal in length. Sheldrick, cited in Laws (1966), reports that appearances of the first and second tusk through the gingivae in a tame female elephant calf were separated by seven months. Though the data sample is small, it indicates that, from the start, tusk pairs are not necessarily mirror images of one another. However, average tusk pair lengths and weights of elephants over 6.5 years of age assembled in five-year cohorts showed no significant statistical length or weight differences between the right and left tusks in either gender. Nevertheless, pairs of exactly equal length and weight are greatest early in life and decrease slightly with age, which is not unexpected over ~60 years of life, wear and use. Presumably, the ‘congenital’ differences noted in elephants < 5.5 years old are too small to be detected in the measurements taken or are evened out by use, for which there is much evidence (see below).

Versace and Vallortigara (2015) report that preferentially using either right or left sides occurs across the animal realm in both vertebrates and invertebrates including humans. Long-standing lore among hunters and traders is that elephants use one tusk preferentially in the manner of handedness in humans. The findings presented here contradict that perception. They also, for example, contradict the observations of Hall-Martin, who used the term ‘servant tusks’ for the lighter in a pair (Bosman and Hall-Martin 1986; Raubenhmeimer et al. 1989; Bielert et al. 2017). With tusk weights as their only measure in examining lateralization, Bielert et al. (2017) found that 94.29% of right tusks were lighter than left tusks and, without considering other possible causes, attributed this to preferential use. Their data were 683 “sportsmen’s” trophy tusk pair weights that originated in 16 different African countries between 1955 and 2010 and included both elephant species, i.e. *Loxodonta cyclotis* and *L. africana*. Their mean weights of right and left tusks, respectively, were 30.24 and 30.65 kg. This difference of only 0.41 kg or 1.3% of the heavier weight challenges their assessment of significant difference. They noted, but did not explore, that the heavier of a tusk pair was sometimes the shorter. They did not test the possibility that the identification of a tusk as ‘right’ and ‘left’ may have been determined by the myth of ‘handedness’ itself—a possibility, given how deeply set it was in hunters’ lore.

Whyte and Hall-Martin (2018) detected no such lateralization in weights of tusks of 271 females or 200 males when analysed separately, but when the sexes were combined there was a slight bias for ‘right-tuskedness’. They sought no support from such lengthy data as they had; nor did they consider the possibility that ratios between right and left might alternate through an elephant’s life or be affected by any other dynamic. Their combined total of 471 was only 20.5% of the 2,305 sampled here, where both length and weight presented in five-year cohorts showed no such bias, suggesting their sample in animals living >50 years was too small.

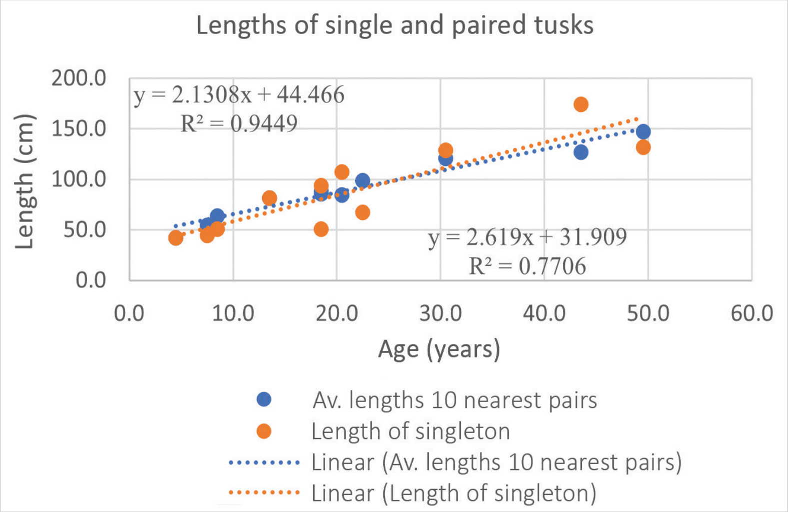


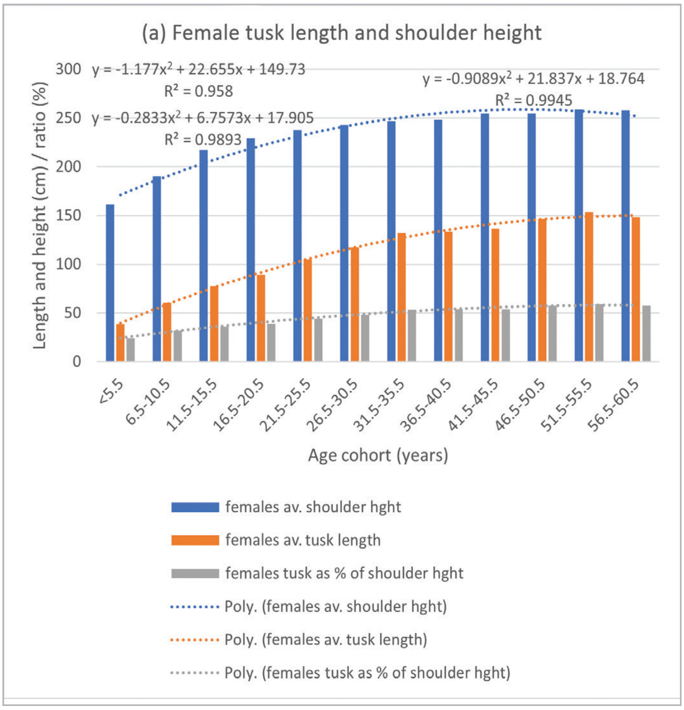
Figure 11. The length of tusks of single-tusked females in herd GMU 32, compared to the average lengths of pairs of tusks of 10 females closest in age to them. Dotted lines show linear regression equations.

Table 9. The shoulder heights and lengths of the longer tusk in 294 female tusk pairs and 269 male pairs, and tusk length as a percentage of shoulder height, presented as averages in five-year cohorts.

Age class (years)	Females			Males		
	Shoulder height (cm)	Tusk length (cm)	Tusk length as % of shoulder height	Shoulder height (cm)	Tusk length (cm)	Tusk length as % of shoulder height
<5.5	161.1	38.3	**23.8**	166.8	43.6	**26.1**
6.5–10.5	190.3	60.4	**31.7**	197.2	76.9	**39.0**
11.5–15.5	216.9	77.6	**35.8**	219.0	96.9	**44.2**
16.5–20.5	229.4	89.2	**38.9**	254.0	122.8	**48.3**
21.5–25.5	237.7	104.9	**44.1**	270.0	141.6	**52.4**
26.5–30.5	243.1	117.1	**48.2**	287.5	155.4	**54.1**
31.5–35.5	246.6	132.0	**53.5**	307.3	183.6	**59.7**
36.5–40.5	248.4	133.3	**53.7**	304.0	230.0	**75.7**
41.5–45.5	254.3	136.7	**53.8**	300.8	203.7	**67.7**
46.5–50.5	254.3	146.6	**57.6**	323.5	198.0	**61.2**
51.5–55.5	258.7	153.2	**59.2**			
56.5–60.5	258.0	148.3	**57.5**			

Summarizing the data of both genders, in ~80% of pairs of tusks the longer tusk is heavier, in 5–6% of pairs the heavier tusk will be the shorter and in 8–9% both length and weight will be equal. However, these differences are equally distributed between right and left. Data on neither length nor weight of average tusk pairs assembled in five-year cohorts support the idea that elephant tusk pairs reflect neurally lateralized use, similar to human right- or left-handedness.

However, this does not mean the phenomenon is absent in elephants: only that if it occurs, the dynamics of tusk growth and wear (discussed below) conceal it. It might be better looked for in how they use their



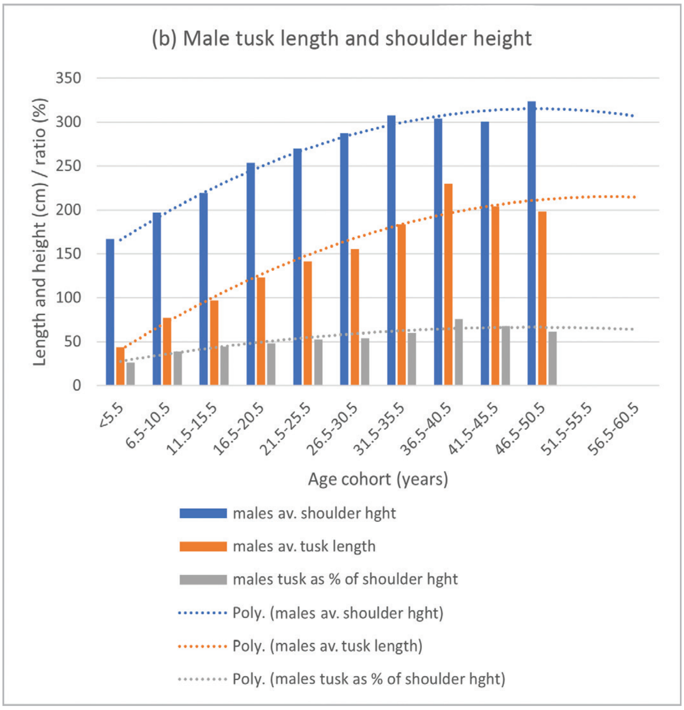


Figure 12. Average shoulder heights and longest tusk lengths, and tusk length as a percentage of shoulder height for (a) female (n = 294) and (b) male (n = 269) elephants. Cohort ages are averages, i.e. 8.5 = 6.5–10.5, 13.5 = 11.5–15.5, etc. Dashed lines show curvilinear fits based on second-order polynomial regressions.

feet which, despite lacking primate-like digits, are used for scuff-digging, forwards, backwards and sideways, both forcefully or gently, or using 360° of the rims of both front and rear feet with surprising sensitivity to gently explore an object (pers. obs. 1960s). Further, suggestion of a bias towards the right has been observed in how elephants use their trunks (Lefeuvre et al. 2021).

Tusk shapes

While length and weight at age differentiate male from female elephant tusks, their shapes also separate the genders. Long-known to traders and hunters, this experience-based albeit subjective knowledge is illustrated in Figures 5 and 6. The data presented here extends and confirms Elder's (1970) observations. Measurements of tusk base and lip diameters within the alveoli before they have been exposed to external influences confirmed that the female tusk is more or less cylindrical until aged in the mid-20s, after which its base circumference starts gradually shrinking. In males, the initially strongly tapered alveolar shape is retained until around the mid-20s. From this age on, the taper decreases until after the 40s, when the base:lip ratio gradually becomes negative. Photographic data support Whyte and Hall-Martin's (2018) observation that female tusk growth declines in late age, which is cautiously suggested in Parker (2024). The photographic evidence indicating that a similar decline also takes place in male tusks contradicts both Laws' (1966) and Whyte and Hall-Martin's (2018) assertions that there is no fall-off with age in male tusk growth. However, caution is advisable in accepting findings from so small a data set. This apparent declining tusk growth in late life requires confirmation based on more comprehensive evidence.

Elder (1970) reports changes in tusk pulp volumes with age. Parker (1979) records a decline of pulp volume from 820 ml around the end of the female's fourth decade down to 300 ml in the late fifth decade, with pulp being replaced by dentine. Whyte and Hall-Martin (2018) found a similar regression from a maximum pulp volume of 785 ml coinciding with age 41 years, when the average weight of tusks was also at its maximum. While not giving pulp volume minima after 41 years, they also report its replacement with dentine. This contraction of tooth pulp volume and substitution by internal dentine is not apparent from external shape and weight. Presumably, pulp reduction is accompanied by diminished activity of dentine-producing odontoblasts, explaining Whyte and Hall-Martin's (2018) findings of a decline (but not cessation) of female tusk growth after age 41. Comparable data from male tusks were not available (vis-à-vis we do not have comparable data on pulp regression from males). If the replacement of pulp volume by internally deposited dentine exceeds the rate at which tusks are extruded, this might explain the findings of both Laws (1970) and Whyte and Hall-Martin (2018) that exponential male growth, when measured by weight, was uninterrupted. If pulp volume and length had been their measures of tusk growth, they would have found otherwise. The fact that there is a reduction in male pulp with age is hinted at by East African professional trophy hunters who could accurately judge the lengths and girths of the tusks, but with the caveat that weight "depended on the size of the nerve [pulp]". Personally, having looked into the pulp cavities of many hundreds of big tusks, I can confirm that there is much variation in volume. This subjective recall would also be consistent with some degree of pulp decline. The evidence of tusk pulp volume regressing in both genders is persuasive but still needs definitive confirmation.

Tusk growth

The finding that the weights of single tusks are not less than those of tusk pairs of similar ages, despite single tusks having to do the work of two, implies that the tusk sizes are determined by factors other than normal wear and usage. This determining factor appears to be the size of the animal (considered below).

The photographs showing the two-dimensional shape of tusks of herds GMU 30 and GMU 32 (Fig. 9) are missing any spiral dimension, either supporting or contradicting Laws' (1970) assertion that tusks grow in logarithmic or helical spirals. This feature of proboscidean tusks is mentioned by Larramendi (2023) with reference to Evans et al. (2021). Nevertheless, the photos suggest a genetically transmitted curvature common to herd members in accordance with Moss and Poole's (1983) finding that members of such units are closely related, many being the matriarch's direct descendants. This was the basis for the assumption made in this study that since GMU 32 females are the matriarch GMU 235's daughters or grand-daughters their tusks represent images of what her tusks would have been like at their respective ages. While conscious

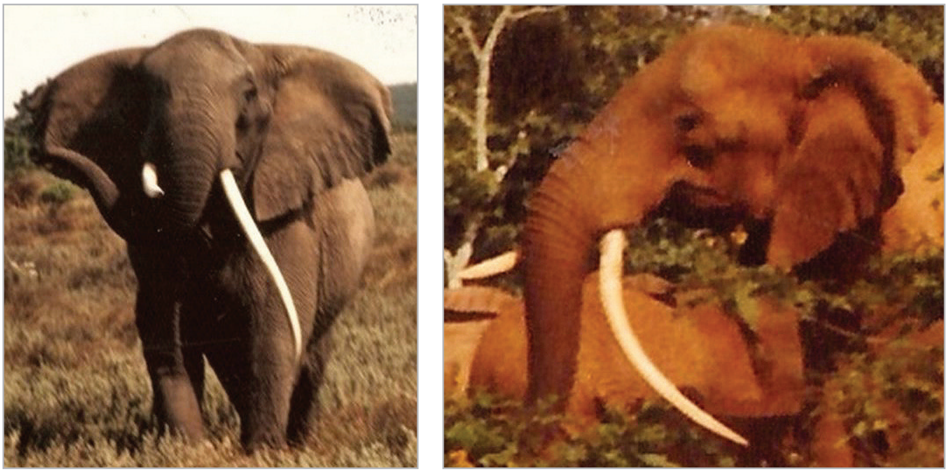


Figure 13. Two views of the same elephant illustrate a tusk oriented so that it could not be used as a tool and thus not subject to wear, as was its partner. The only loss of length would have been through weathering. (© AMD Seth-Smith).

of having only one example where much larger samples would have been desirable, the results presented here give an insight into the discrepancy between Laws' (1970) putative average asymptote for female tusk length of 510 cm and Parker's (1979) measured average maxima of at 60 years of only 160 cm. It is evidence that at all ages after losing the enamel cap, tusk dentine is being eroded and at 50 years female elephants may have grown and lost much more ivory than is present in the tusks they carry.

Empirical supporting evidence comes from Figure 13, showing a female whose left tusk was either congenitally or traumatically rotated in its alveolus so that it curved backward continuing to grow but could not be used normally. Freed from use (but not weathering), it had grown towards its potential length. The backward curving tusk's partner appears typical and from the finding that single tusks are not shorter than paired tusks, the disparity between the two gives some idea of what the shorter tusk may have lost through use and wear. The fact that such cases are rare may be because the tusks would be obstructions and likely to be accidentally broken or shed. Figure 14 depicts a similar case recorded by Joyce Poole in the Mara area of Kenya.

Tusk wear

The reason why tusks never reach their theoretical asymptotes is explained by wear. Devoid of contact with the blood supply or any means of replenishment from the tooth pulp, for all practical purposes, tusk outside the skull is dead tissue and can only lose matter. Replacement and augmentation by growth and

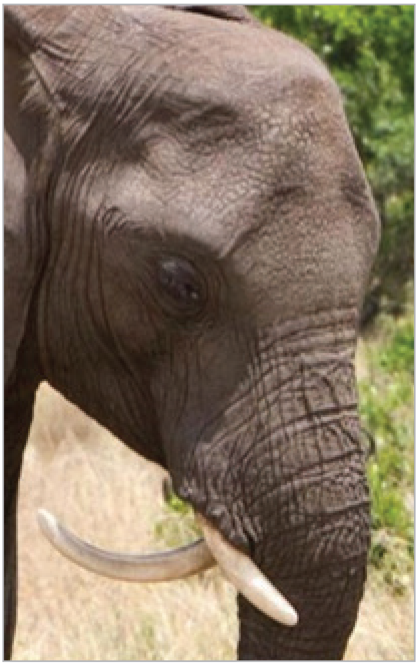


Figure 14. A similar case to Fig. 13 is the above photo of a juvenile elephant, with a tusk rotated in the alveolus, either congenitally or traumatically, so that its curvature prevented normal use.
(© Joyce Poole).

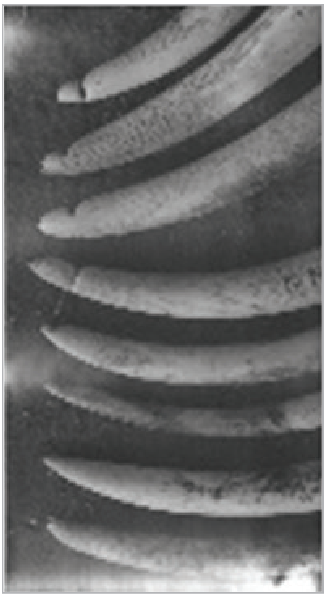


Figure 15. Tusks (from Murchison Falls NP) showing 'shakes' (see text) and the notching that results in tusk tips breaking off. The tips of the second and fourth tusks from the top show evidence of recent breakages.

further extrusion originates within its alveolus (Raubenheimer et al. 1990). Dentine's relative softness renders tusks subject to loss from decomposition, abrasion, chipping, notching and transverse fractures. Chipping occurs when small bits of ivory break off tips, for example when digging into hard substrates. The degree to which elephants are prepared to do this was illustrated by three males who were seen digging pieces out of a concrete floor that were then ingested (Hinga Muigai, pers. comm. 1994).

Ivory decomposition is most obvious postmortem (pers. obs. 1960s). Exposed to the elements, its smooth, glossy surfaces progressively become rough, powdery, chalky and eventually crumble to a powder. Depending on multiple environmental factors including tusk size, this decomposition may be rapid and destroy a small tusk in less than a year, or in larger specimens slow and take several decades (Parker and Graham 2020). Yet, it will have commenced while the animal is still alive, with the effects of constant abrasion in use and rubbing with the trunk seen in the smooth surfaces of the tusks of living animals.

Weathering, due to the combined effects of insolation, temperature, humidity, etc., of a tusk's exposed surface is part of the foregoing process. Because of dentine's poor thermal conductivity (Jakubinek et al. 2006), these influences do not penetrate deeply into the dentine matrix. In addition, since dentine is slightly flexible, compression and expansion stresses during use will also be greatest around the circumference of the tusks, i.e. at the surface. Combined, these stresses produce fine longitudinal, hairline cracks that penetrate tusks radially and were called 'shakes' or 'streamers' by ivory craftsmen (Fig. 15).

On the living animal and in freshly extracted ivory these cracks are seldom more than 1 mm deep, progressively becoming more abundant toward tusk tips, presumably the result of longer exposure and the tusk becoming thinner toward the tip and thus more vulnerable to flexure. By allowing extraneous matter, such as plant saps and soil, to penetrate the surface and acquire and lose moisture, 'shakes' are not only produced by but also contribute to decomposition. Until post-mortem, they do not extend into a tusk's protected alveolar sections where growth occurs, and where tissues are alive and have a blood supply. After death and on leaving a dead elephant's skull, shakes deepen radially inward toward the tusk core, extend in length, appear in the alveolar section, and eventually develop into multiple longitudinal splits.

Notching (Fig. 15), mentioned by Capstick (1977) and Raubenheimer et al. (1989), produces tip-snapping. Notches are usually apparent within the 15 cm of a tusk's tip. Feeding elephants use their tusks as fulcra, over which they drag and break vegetation, which is caught up in nicks or faults in the tusks' circumferences or depressions produced when an ivory 'bean'[1] drops out, creating grooves or notches that, as they grow, progressively snag more material. Their development accelerates until, when stressed, the tip breaks off, leaving only a small rough breakage area that is quickly smoothed back to a point. If Laws' (1970) estimates of the annual growth of female and male tusks are of the right order (respectively 8.5 and 11 cm), then a notch loss could remove a year

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[1] Ivory 'beans' or 'pearls' are independent dentine bodies usually developing near the apex of the tooth pulp, usually small (~1 cm) in diameter but occasionally much larger, that become embedded in the tusk matrix, carried forward by the tusk's outgrowth and, when the retaining dentine around them wears away, drop out leaving a hollow.

(a) August 1998

(b) October 2011

(c) October 2011

(d) Later October 2011

Figure 16. Photos of elephant f0096 in Maasai Mara, Kenya, showing tusk changes over a period of more the 13 years, from a transverse break in the right tusk coupled with evidence of notching.
(a) In 1998 a transverse right tusk break coupled with a developing left tusk notch.
(b) By 2011, thirteen years later the right tusk in a) with a developed notch, now longer than the left tusk.
(c) The left tusk in b) enlarged to show a developing notch that is less than the left tusk notch in a), and clearly younger.
(d) The same tusk as in b) and c) but later in the same month showing how much the notch in c) has grown.
© Joyce Poole.

of growth in both genders. Although notching was only entered on culling field data sheets as an occasional note, it was recorded from 17 females and 11 males, with 48% and 52% of all notches found on right and left tusks respectively, again supporting evidence of even use. However, the incidence of notching was much higher than occasionally recorded on the culling data sheets. In a photographic sample of 235 tusk tips across a range of tusk sizes, 86% showed ends characteristic of chipping or notching having occurred (Parker unpublished data). Figure 15 supports this, showing eight tusk tips with notches and/or evidence of chipping. If tusk pairs grow at around the same rate and there are no statistically significant length and weight differences between average right and left tusks, both sides must be equally vulnerable to chipping and notching. Since this is unlikely to happen in both tusks at the same time, it follows that over time the longer tusk will alternate between right and left. The results will only be apparent from repeated observations of the same animals over long periods. Nevertheless, an unavoidable conclusion is that substantial dentine loss is not occasional but a constant feature of the average savannah elephant tusk.

Transverse fractures occur when a stressed tusk snaps across its longitudinal axis anywhere between the tip and the lip, excluding notching. However, while occurring in only 8% of a sample of 1,525 tusk pairs (Parker 2024) and contributing to dentine loss, they are most likely unpredictable stochastic accidents, and there is no evidence that most or all elephants other than fighting males will experience them, though that has to be proved.

Fig. 16 images from Elephant f0096 from the Mara in Kenya observed by Joyce Poole: Panel (a) August 1998, illustrates a transverse right tusk break and a left tusk notch. Panel (b) from 2011 shows a recovered right tusk length with a notch already starting to form, while the left tusk point suggests some loss between (a) and (b), with a new notch already developing, as shown close up in Panels (c) and (d). These repeated breakages make it impossible to measure relative growth rates between right and left.

Fig. 17 shows the tusks of an Amboseli male elephant named Tolstoy whose life was followed from birth in 1971 to his death from natural causes in 2022 aged 51. In Panel (a) he was 35 years old and both tusks were near parity in length. In Panel (b) four years later, aged 39, his right tusk had lost more than 40% of its length through a transverse break, presumed from fighting. Panel (c) shows how over the next three years not only had the broken tusk recovered considerable length, but its ragged break had worn back to a blunt rounded point. In Panel (d) the left tusk was now shorter than the right tusk, having had a substantial portion sawn off by the Kenya Wildlife Service, apparently for cosmetic reasons. For this study, it was the equivalent of a natural transverse break. Panel (e), a photograph taken a year before he died, shows that over the preceding seven years not only had right and left tusks grown considerably longer, but they were once again close to parity.

Figs. 16 and 17 are individual cases that illustrate savannah elephant tusk dynamics and their complexities. Both reflect broken tusks catching up and regaining parity in length with their partner tusk, whose length is set by the bearer's shoulder height. With the broken tusk not being used, its circumference at the break will be carried forward without wear until once again long enough to come into use. During this recovery in length the lack of wear would result in circumference inequality between pairs, and account for a shorter tusk sometimes being the heavier of a pair as reported by Bielert et al. (2017) and as shown in Table 5.

Tusk length and body size

This population perspective of parity between tusks of a pair and their correlation with the elephant's shoulder height is facilitated by extravagant continual tusk growth (though not necessarily at constant rates) throughout life. Its evolutionary value seems to lie in the physics of providing a tool that fits the size of the user, in turn determined by behaviour. It explains why elephants in Kenya, north-eastern Tanzania, and much of Uganda have tusks that are so similar and match their heights. Climate, geology and habitat undoubtedly influence rates of growth (Laws et al. 1975; McCullagh 1969) and wear, but these influences are concealed by the latitude provided in the huge disparity between potential and actual lengths. The evidence presented here explains the difference between Laws' (1970) and Parker's (1979) length asymptotes.

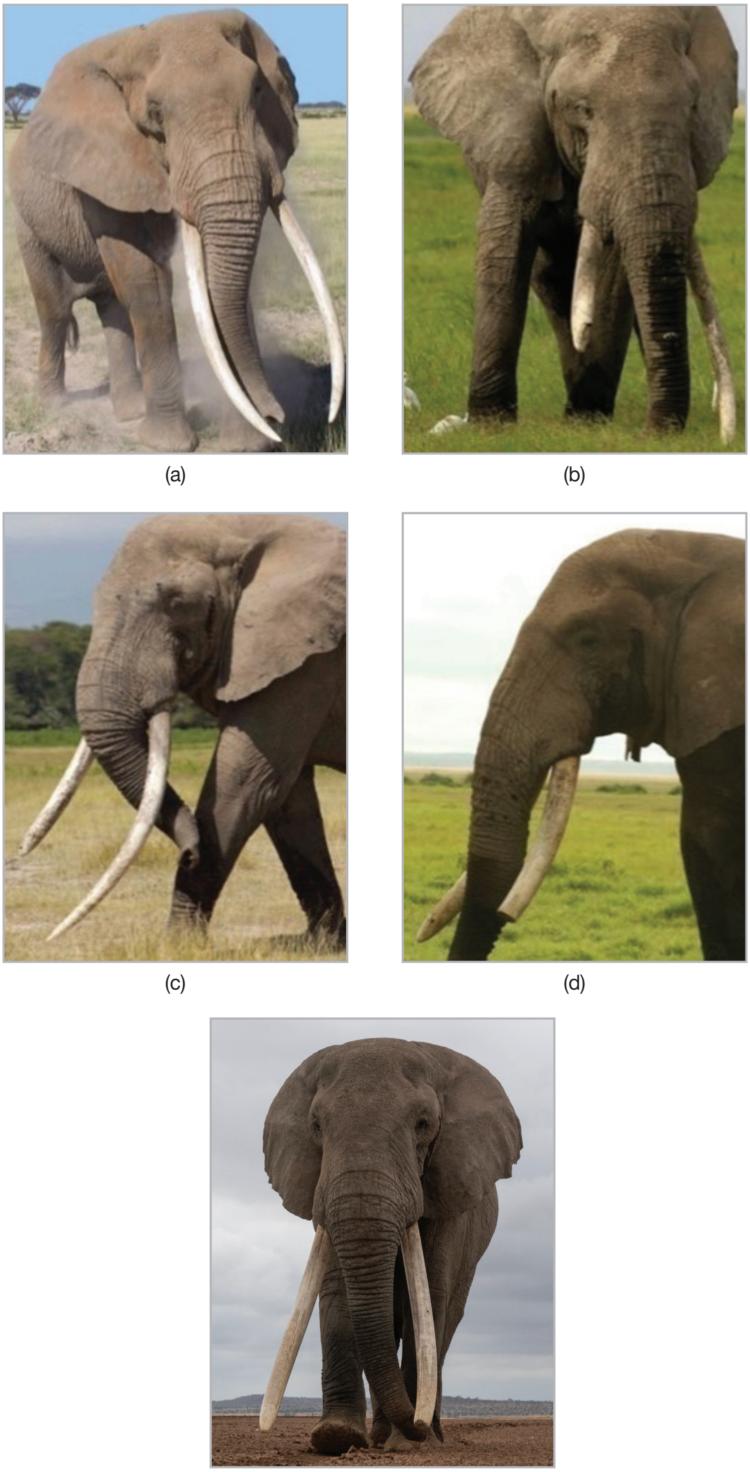
These findings should be extrapolated cautiously beyond East Africa, particularly as Elder (1970) was moved to write his paper on subjective but consistent hunters' reports that elephants in Botswana were different to those in East Africa. Parker (1979) subjectively recognized four continental tusk types: Sahelian, Cyclotiform, South-western and East African. Bosman and Hall-Martin (1986) noted that elephants from different parts of Africa varied in body size, tusk form and length and ear shape. Raubenheimer et al. (1989) also asserted that the size and qualities of tusks from different parts of Africa varied, but only documented dissimilarity between Namibian (Parker's South-western type) and the Kruger NP ivory (Parker's East African type).

Acknowledgements

For the acquisition of my knowledge of elephants and their tusks, I am indebted to too many to list, including the Wata elephant people of eastern Kenya, game wardens and scouts, biologists, and ivory traders, and my gratitude for their contribution is immense. Particular thanks to statisticians Brian Reilly, Rowan Martin, and, especially, Don Franklin and John Ludwig for struggling with my congenital innumeracy. Joyce Poole generously let me use material from her copious data bank. Phyllis Lee provided useful information. And again, to my wife Christine for encouragement.

Data availability

All the raw data from the five elephant clans cited in this paper are available at:
http://ufdc.ufl.edu/AA00013409/0007



(a) (b) (c) (d) (e)

Figure 17. Photos of the Amboseli male elephant ‘Tolstoy’ at five points in his life to illustrate tusk recovery in length after major transverse breaks.
(a, b, c and d) © Joyce Poole/Amboseli Trust for Elephants; (e) © Federico Veronesi)

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