

The missing metric: speculations on tusk curvature

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Abstract

As weight is the criterion of commercial value, elephant tusks have been weighed in their millions across the centuries. More recently, it has been shown that weight, length and circumference-at-lip of the African savannah elephant (*Loxodonta africana*) are predictive of one another and, at the population level, related to age. Missing altogether are data on the curvature created by helical tusk growth. Describing this in population terms would require large sample sizes of tusks from both sexes of all ages. While natural mortality of elephants of known ages could, in due course, provide sufficient data for such an analysis, at present none are available. To partially fill this knowledge gap, this paper considers available evidence to suggest how the shape of the male savannah elephant tusk changes with age and how its changing curvature may influence behaviour.

Résumé

Le poids étant un critère de valeur commerciale, les défenses d'éléphant ont été pesées par millions au fil des siècles. Plus récemment, il a été montré que le poids, la longueur et la circonférence (mesurée au niveau de la lèvre) des défenses de l'éléphant de savane d'Afrique (*Loxodonta africana*) sont des données prédictives les unes des autres, et, à l'échelle de la population, sont liés à l'âge. En revanche, les informations manquantes concernent la courbure créée par la croissance hélicoïdale des défenses. Pour décrire cela en termes de population, il faudrait disposer d'échantillons importants de défenses provenant des deux sexes et de tous les âges. Si la mortalité naturelle des éléphants dont l'âge est connu pourrait, à terme, fournir assez de données pour une telle analyse, elles ne sont, à l'heure actuelle, pas disponibles. Afin de combler en partie ces lacunes, le présent article examine les données probantes existantes pour suggérer de quelle façon la forme des défenses des éléphants de savane mâles change avec l'âge, et comment la modification de leur courbure peut influencer le comportement de son propriétaire.

Introduction

Einstein (1931) observes that “imagination is more important than knowledge. For knowledge is limited, whereas imagination embraces the entire world.” Yet while some imagination seems mystical, most inventions and ideologies are self-evidently stimulated by knowledge. Using the data available to me, I propose a hypothesis to fill a knowledge gap about the role tusk curvature plays in the behaviour of male African savannah elephants (*Loxodonta africana*).

In what follows, the knowledge of elephants and their tusks underpinning my speculations is grounded in both objective analysis of data from 2,900 elephants culled in Uganda, Kenya, and Tanzania (Parker 2024a; Parker and McCullagh 2021), and the subjective experience of observing elephants and handling over 100,000 elephant tusks in 14 African and eight Eurasian countries between 1956 and 2014. While I never tallied the numbers examined in traders' vaults, artists' workshops, the houses of trophy hunters, government stores or the international ivory marts of

Africa and Eurasia, they must run to hundreds of thousands. I think I am familiar with tusks.

Tusks that I observed in living elephants and post-mortem displayed wide differences in shape and size, for which there was no obvious explanation. Some seemingly old elephants had only short tusks, while those of supposedly young individuals were long; similarly, some individuals of the same age had thick tusks and others thin ones. However, such perceptions were based on observations of a few individuals, whereas establishing population norms in animals that can live for more than 60 years calls for large samples from all ages. It was not until Laws (1966) established that age and sex predictably govern tusk weight that a sense of order emerged. I expanded on that order (Parker 2024a; 2024b), showing that the average length and circumference-at-lip are commensurate, and that weight, length, and circumference are mutually predictive of one another. I further explain the differences between theoretical and actual asymptotes, which arise through wear and breakage, and how average tusk lengths are related to an elephant's height (and thus the length of its bones). Yet, while age, growth, shoulder height, tusk weight, length and circumference-at-lip correlate closely, shape does not. The reason for this is that tusks are not simple arcs but grow as spirals. This breaks the symmetry between tusk pairs displayed by the other metrics. Continuously growing from its base, in the alveolus, a broken tusk will recover lost length and catch up with its partner. The break will be worn back to a point, and the lost length recovered. However, the curve of the lost piece of tusk cannot be replicated. This results in the orientation dissymmetry we commonly see in living elephants. Yet while obvious enough, hard data describing curvature are lacking to explain this phenomenon. To partly fill this gap, I exercise my imagination and focus on how curvature affects the tusk shape of male savannah elephants and how this, over time, affects their value for fighting.

Hypothesis

Parker (2023a) observes, *inter alia*, that in an animal with continuously growing structures and

a longevity spanning decades, as with humans, large samples are essential to establish population metrics. Applying this maxim, the author analysed a sample of 946 male savannah elephant tusks out of the total 2,900 culled and derived asymptote values of ~250 cm length and 40 kg weight (Parker 2024a). These are far below maximum values of >335 cm length and >100 kg weight for individual tusks given by Balan (2025 *in litt.*) in his compendium of record tusk metrics. Such maxima are widely assumed to be 'normal' and attainable by elephant bulls who live beyond 50 years. Furthermore, their rarity is taken to be a consequence of selective hunting for big tusks. However, Parker (2023a) points out that male elephants over 50 years of age whose tusks attain asymptotic lengths and weights represent <1% of elephant populations, even in Murchison Falls National Park (NP), where elephants had not been hunted for more than 50 years. Whether this low survivorship of old males with large tusks applies beyond the range of 'East African type elephants' as described by Parker (1979) is moot.

Unpublished ancillary evidence supports the rarity of old male elephants with tusks weighing >40 kg. In 1965, Uganda's Murchison Falls NP held ~14,000 elephants. In the open habitat where elephants were easily and regularly observed from both ground and air, such tuskers (some individually named e.g. *Tangi Monster* and *Lord Mayor of Paraa*) were certainly fewer than 50 (0.4% of the population). Similarly, in South Africa's Kruger NP in the late 1970s, only six such exceptional tuskers were known, namely *Mafunyane*, *Shawu*, *Shingwedzi*, *Dzombo*, *Hlanglene* and *Kambaka* (Raubenheimer et al. 1989; A. Hall-Martin, pers. comm., 1985) accounting for <0.1% of the total elephant population of ~7,000 individuals. Wherever males with tusks exceeding 40 kg became known, they attracted the attention of hunters and conservationists, who commented on both the size of the tusks and their rarity. For organizers of commercial safaris at the turn of the 20th century, securing tusks over 40 kg was both a goal and ground for comment when achieved. Incomplete as such evidence may be, it nonetheless gives grounds for confidence in the findings from the 2,900 culled elephants that male tusks rarely exceed 40 kg weight. Contrary evidence is provided by photographs¹ taken across the past 150

¹As shown in Simon Trevor's monumental documentary series Tsavo: *A Moment in Time* (2024) listed in References



Figure 1. How I imagine the tusk shape Laws (1966) describes. © Travis Tischler.

years of many male tusks of >40 kg on warehouse floors, which are presented as proof that such elephants were once common. The evidence establishes abundance, which is hardly surprising given that elephants occurred in virtually all biota of sub-Saharan Africa. Yet this abundance of large elephant tusks does not challenge the finding that old male savannah elephants form very small proportions of their populations.

Obtaining statistically robust data from reliably aged male African elephants older than 40 years is not possible. A further complication is the probability that metrics on any parameter may differ regionally (Elder 1970; Parker 1979). All the foregoing has a bearing on any analysis of the savannah elephant tusk curvature—the missing metric—and how it might influence behaviour.

Curves abound in nature and in proboscidean tusks in particular (Hayden and Fisher 2011; Evans et al. 2021). Laws (1966) said that East African savannah elephant tusks grow continuously throughout life in logarithmic or helical spirals. Figure 1 below illustrates what I imagine Laws had in mind.

My personal subjective observations confirm this view. Moreover, the spirality is usually chiral; that is, the tusks are non-superposable mirror images of one another. However, as illustrated in the photographs of 165 pairs of tusks from 15 culled herds laid out on flat ground and taken vertically, in two dimensions they appear as simple inward arcs without the third dimension of depth (Fig. 2).

All aspects of an elephant's tusks are obviously determined by an overarching genetic template. Yet within these limits, there is wide variation. Most herds composed of females and immatures are families (Moss and Lee 2011) and similarities among their tusks reflect genetic influences (Parker 2024a, Fig. 9). However, genetic differences among herds in the sample in Figure 2 are not so obvious, and the tusks in the different photographs appear more similar than dissimilar. As presented, they seem to be simple arcs,

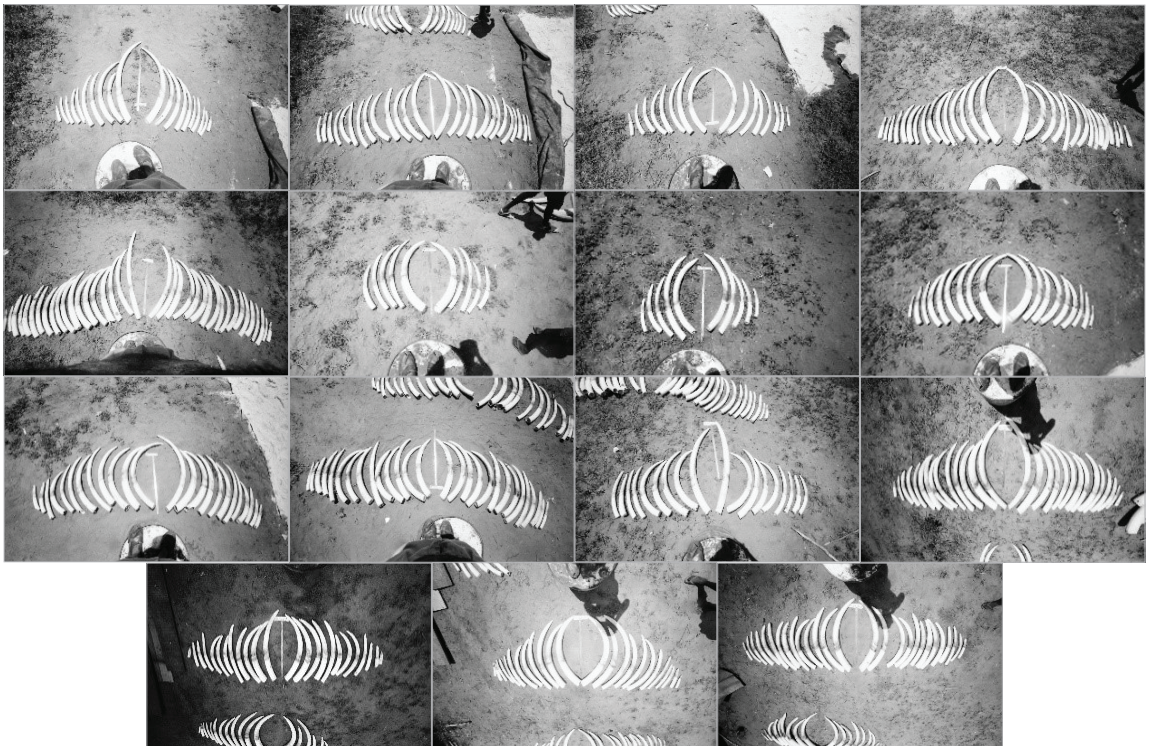


Figure 2. Tusks from 15 herds culled in Mkomazi East Tanzania laid out on flat ground and photographed vertically from above.



Figure 3. An exceptional illustration of helical tusk growth. © Suzannah Goss.

whose depth is found by drawing a line at a right angle from the centre of the chord connecting the two ends until it meets the arc. This is the arcuate tusk form of popular perception. However, the two-dimensional view conceals the third dimension of the helix. With a helix, the equivalent line connects the axis of the helix to the arc; its length is the radius of the helix, and it rotates in accordance with its direction (clockwise or anticlockwise).

Having closely inspected and handled many tusks from elephant of all ages, I believe the helical twist is intrinsic to all savannah elephant tusks in both sexes. However, the radius of the helix increases with age and is close to zero in young elephants. Thus, the helical curvature does not become apparent until it is well developed in older elephants as the tusks approach their asymptotes. Since data on three-dimensional tusk curvature are very rare, I use evidence from old elephants with tusks longer than the known population means to illustrate helical growth. Figure 3 presents an extreme case where, as the tusk grew, its tip rotated through more than 360°. Such growth in the savannah elephant tusk is anomalous, and this the only one I have seen in more than 200,000 tusks. Yet, as pointed out by

Lister (*in litt.*), such curvature recalls male mammoth tusks.

Less extreme is a pair of tusks displayed in the Natural History Museum, London, shown from various angles in Figure 4 to illustrate their helical growth. It is notable that in panels (h) and (j) the tusk on the left appears as a simple arc. However, panels (a) and (e) show clearly that this is not the case. Viewing the tusk from different angles reveals the third dimension of depth.

I do not have data on helical tusk growth in African forest elephants (*Loxodonta cyclotis*)—although this does not imply its absence. As evidence from male savannah elephants aged 50 years or older is scarce, given the similarities between their tusks and those of old male Asian elephants (*Elephas maximus*), I sought proof that it occurs in Asian elephants. The instances shown in Figure 5 are from captive animals. The helical curvature is very marked, possibly because the tusks of these captive elephants have preserved more of their natural shape in captivity, where elephants are shielded from tusk loss through use and wear in the wild, and particularly from the effects of combat with rivals. Further, as captive Asian elephants are smaller than wild elephants (Sukumar et al. 1988), this may possibly be reflected in their tusk growth. Comparison of data on African and Asian elephant tusks is difficult, as the two species exhibit different population age structures and ageing processes. Nevertheless, although the male Asian elephant tusk is more slender and lighter than the male East African savannah elephant's tusk, it is basically similar, with growth following a helical path as apparent in the photographs.

Having established that helical tusk growth occurs in males of both East African savannah and Asian elephants, I now speculate on the behavioural value of curvature. Kingdon (1979), referring to the male savannah elephant, considers “the mature male skull as a structure adapted to fighting”. Generalizing, combat between males for dominance and access to females occurs widely in the animal realm and, while the ability to kill an opponent may exist, the purpose is usually achieved when one combatant flees. Savannah elephant males seem unusual in going beyond chasing a competitor away and are known to actually kill their adversaries using deep, penetrating tusk thrusts into vital organs. Hall-Martin (1987) observed that in the Addo NP in South Africa, seven out of the 14 adult males in the Park were killed by other males in musth. Losing or seriously breaking one tusk would



Figure 4. A pair of mounted tusks at the Natural History Museum, London, illustrates how perspectives in two dimensions can hide the third dimension of depth and helical growth. Photos (d) and (h) show the angles of view that reveal maximum curvature. © Adrian Lister.

not necessarily be a disadvantage, but losing both would be fatal unless the adversary was physically much lighter (see below). Such an instance in the Addo NP was reported by Hall-Martin (1987) as follows: “In one case a bull broke a tusk while killing a non-musth male, broke off the remaining tusk while killing a female and, now tuskless, was itself killed by another musth bull.” He recorded a case in the Kruger NP, where a male in musth pursued a larger male not in musth for four days before closing in and killing it (A Hall-Martin, pers. comm., 1990). Poole (*in litt.*) states “...having seen many fights—the victor *always* [my emphasis] chases the loser, often for kilometres”. Simon Trevor’s impressive film record from Tsavo NP (“Tsavo: a moment in time”²) records several of these chases, where the victor uses scent to track down an opponent that has fled out of sight. Trevor was never able to document the conclusion of such chases. However, such a pursuit, when the loser is out of

sight, is not ‘display’. Logically, it must be with the intent to inflict harm.

In the East African ivory trade, pieces of broken ivory recovered in the field (which, from size could only have been lost in male combat) were sufficiently frequent to have their own trade category: ‘chinai’. (This was the term used in the Mombasa ivory auctions, whose market was China) (Parker and Graham 2020).

In Bardia NP, Nepal, Lister and Blashford-Snell (2000) recorded that one of two male Asian elephants seen regularly together suffered a fatal tusk wound into its skull, which could have been inflicted by its erstwhile constant companion. While dealing here with extant elephants, their many morphological similarities with mammoths (genus *Mammuthus*) and mastodons (genus *Mammut*) invite seeking evidence of fighting among their remains. Hormones preserved in fossils (Cherney et al. 2023) have proved that musth not only featured in male mammoth and mastodon behaviour but was also associated with evidence of wounds that reasonably could only have been inflicted in fighting. In Fisher’s words, “this led me to suggest that adult male *Mammut americanum* engaged in musth battles in which a characteristic pattern of engagement involved lowering the head, followed by

²Trevor S. 2024. *Tsavo: A Moment in Time*, Chapter 10. <https://f.io/SpStOaChapter>



Figure 5. Examples of helical growth of tusks of captive Asian male elephants. © George Dian Balan.

swinging the head upward and forward forcefully, thrusting a tusk tip into the cheek region of an opponent” (Fisher 2008). Such a hooking upward tusk thrust was witnessed by Tom Tischler (pers. comm., February 2025) by a male Asian elephant in Perth Zoo.

Although the outcomes of combats are rarely witnessed, ancillary evidence that it occurs far more frequently than observed cannot be brushed aside. Parker (2023a) observes that in two clans that had been protected from hunting for more than 50 years, male mortality rose steeply between the ages of 30 and 40 years, when individuals should be in their prime. In the absence of other evidence relating death to that age class, he attributed this accelerated male mortality to musth-driven combat (Parker 2023a). That similar increases in male mortality are recorded in three other clans that had been hunted (for trophies) suggests an overstatement of the influence of hunting as the sole or major

cause of the absence of older male elephants.

If the savannah elephant’s tusks were straight lances pointing forwards, with an aggressor’s weight behind both in a thrust, they would inflict double wounds. However, they are not straight but rather curved in opposing directions. Inflicting a penetrating wound with a curved tusk requires combining weight with an upward hooking thrust following the trajectory of its curve, as seen by Tischler and posited by Fisher (2008).

However, if the tips of the tusk pair are close, such a thrust would be countered by the partner tusk being curved in the opposite direction. Theoretically, consider a pair of tusks, evenly matched without breakage or wear. Like cork screws, those with a dextral spiral have to be turned clockwise to penetrate, while those with a sinistral spiral have to turn anticlockwise. Although the helixes in elephant tusks are not as severe or regular as those in corkscrews, the principle is embodied in the opposing helixes.

When the tusk tips are close together, and because their curves oppose each other, they act as safety

mechanisms preventing deep wounds, as with young males sparring. Yet, with increasing age, the tips of the developing spiral grow further apart. The position that I hold, developed in the course of conversations with collaborators, and especially Tom and Travis Tischler (see Acknowledgements), is illustrated diagrammatically in Figure 7, which presents vertical and lateral views of male tusk stages in 10-year age cohorts.

The tips are at their widest apart between 30 and 40 years when the helix curve is upward and outward. It is then that a single tusk can be deployed with the least hindrance from its partner in a lethal, hooking thrust with weight behind it. It is in this cohort that male mortality accelerates steeply (Parker 2023a). Beyond this age, the helix goes ‘over the top’ and begins to curve downward and inward, negating the effect of the upward thrust and, with the tusk tips closing towards one another, making the tusks progressively less dangerous and more unwieldy in combat.

A combat that occurred between two male elephants at Mudanda Rock in Tsavo East NP in late 1956 illustrates how tusk pairs are most dangerous when at their widest. Two Park rangers stationed on a rock above witnessed the combat. About 12 hours later, I visited the site, listened to

their account, and examined the carcass forensically. A small family unit with a large male (A) was leaving the pool below the rock, when a second large male (B) appeared at the run. Bull A wheeled and clashed with Bull B head-on without preliminaries. B’s right tusk went into A’s mouth, through the palate deep into its skull; and his left tusk passed along the right side of A’s head. A reared backward to draw himself off B’s tusk, off-balance, head up and throat exposed. As B’s right tusk was freed, he lunged forward again, driving it deep into A’s thorax above the sternum; his left unopposed tusk passed outside A’s right shoulder. A wheeled sideways right, exposing his left flank, and B lunged again, thrusting the right tusk deep into A’s thorax behind (or through) A’s left scapula, and B’s left tusk, again unopposed, passed under A’s neck. Done for, A fell on his right side and B took off after the female/calf herd. It had not gone more than a few paces when a dikdik (*Madoqua kirkii*) burst out from under a bush near its feet, giving its ‘wheeze wheezy’ alarm call. B wheeled around and, in an apparent paroxysm of rage, charged back to where A, lying on its right side, still groaned. Approaching from A’s back B drove its left tusk through A’s skull, through the occiput, down through the brain and out through the throat just behind the lower jaw: its right tusk passed unopposed down A’s upper trunk. Withdrawing, B then thrust both tusks under A’s back

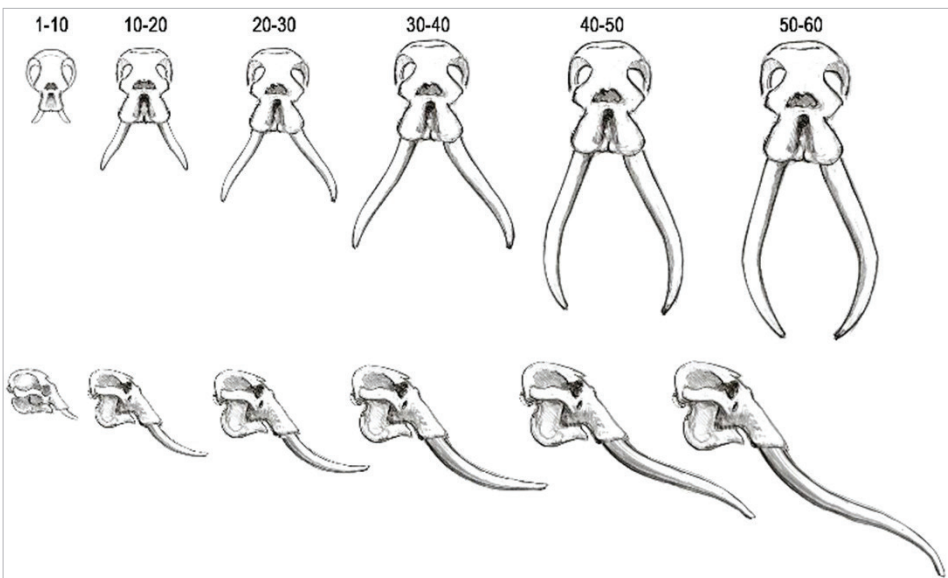


Figure 7. Hypothetical illustrating of helical tusk growth, showing how the tusk tips grow further apart until age 30/40 and then, as the tusks continue to grow, come closer together. © Travis Tischler.

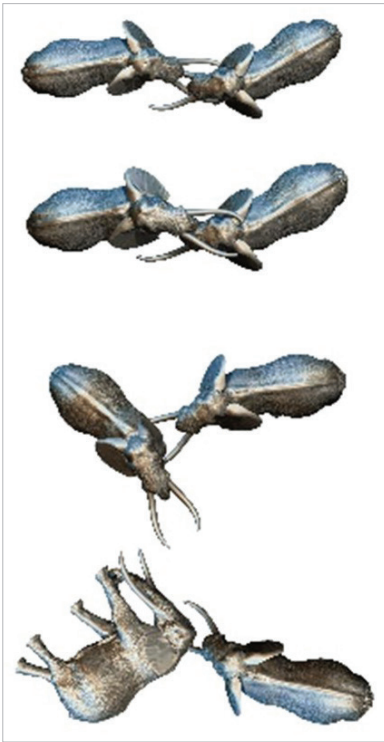


Figure 6. Illustrating the four lethal thrusts made at Mudanda Rock. © Travis Tischler.

and flipped A's body over on to its left side. The whole episode was over quickly and is illustrated in Figure 6. The combatants were both large bulls and likely in musth. The tusks of the vanquished bull weighed over 45 kg and the rangers recalled that the victor's tusks had been both longer and straighter. Instructive was that the four thrusts into the palate, sternum, thorax and skull were inflicted by one tusk, with its partner unopposed and, through curvature, out of the way.

Musth episodes continue into old age (Hollister-Smith et al. 2007), although declining late in life. However, quantitative data at the population level are again hard to come by, due to the rarity of old males. Accepting that musth is hormonally driven, and assuming that a general decline related to old age would be reflected throughout the endocrine system, the few data I have access to indicate that the weight of testes ($n = 1,120$) and seminal vesicles ($n = 291$), and sperm counts ($n = 241$) all decline in the oldest animals (Parker and McCullagh 2021). This reduced reproductive fitness, together with the

declining value of the tusk as a weapon, would place the oldest bulls at an increasing disadvantage when competing with younger, fitter bulls of virtually the same size. If these males are still musth-driven to fight, this goes a long way toward explaining the rarity of old male savannah elephants.

Clearly, from the great rarity of congenital bilateral tusklessness in savannah elephants (Parker 2023b), tusks would appear essential in both ritual and combat for successful reproduction. Here, note has to be taken that congenitally bilaterally tuskless Asian elephant males (Makhanas) can both defeat tusked opponents and mate successfully (Chelliah and Sukumar 2013). However, in such contests, the tuskless winner is invariably the larger of the two (S. Pokharel, pers. comm., April 2025). This highlights the importance of weight in fighting, which can vary greatly between individuals in the same age cohort. To illustrate this point, out of the sample of 946 male savannah elephants (see above), in 11 aged between 41 and 50, the heaviest weighed 5.67 metric tonnes and the lightest 3.74 metric tonnes; that is, the heaviest weighed 52% more than the lightest. Two of the 11 aged 43 years weighed 4.79 and 3.74 metric tonnes; the heavier weighing 22% more than the lighter. When clashing head-to-head, a weight difference of such an order becomes a weapon in itself. Using it, a heavier tuskless animal could keep a lighter tusked opponent off-balance and unable to apply the momentum necessary to deliver a deep tusk thrust. This would explain how a tuskless Asian elephant male could defeat a lighter tusked opponent. In the savannah elephant, where both combatants are likely to be tusked, such weight advantage would be either enhanced or reduced by differences in tusk metrics and orientations.

Sukumar³, suggests that the number of tuskless male Asian elephants in India may be human induced through selective removal of tusked males over millennia. If this can be verified, logically a similar evolutionary process could occur in the savannah elephant. Some support for the idea is given by Campbell-Stratton et al. (2023).

As male elephants, both African savannah and Asian elephant species grow older, their tusks continue to grow as well. In later life, the size and curvature of these tusks eventually compromise their effectiveness

³Sukumar R. <https://www.youtube.com/watch?v=M9GYEV0TTng>

as tools or weapons. In contrast, increasing age compromises their value as displays of virility. This extravagant ivory production automatically invites comparison with other proboscideans extant and extinct.

The straight, downward-pointing and seemingly less curved tusks of African forest elephants (*Loxodonta cyclotis*) would be difficult to employ in combat, (as *L. africana* does with its more forward-oriented tusks), and imply different behaviour. As the two species are known to hybridize, this apparent vulnerability of *L. cyclotis* could lead to its gradual evolutionary replacement by *L. africana*. However, the field of elephant genetics is something of a puzzle, as indicated by the title of Roca's (2019) paper "African elephant genetics: enigmas and anomalies", which convincingly argues that the genetic relationship between the two species is not yet "done and dusted". A piece in this puzzle is the presence of mitochondrial DNA of *L. cyclotis* (i.e. F clade mtDNA haplotypes, where F indicates "forest derived") in many eastern and southern savannah elephants far from the forest elephant's distribution. It challenges the prevailing view that the two species hybridize only in restricted areas peripheral to Africa's equatorial forests. While this view hints at a process of gradual replacement, in these areas, of *L. cyclotis* by *L. africana*, the DNA evidence highlights the need for an understanding of the Pleistocene expansions and contractions of *L. cyclotis*' putative habitat: the Congo Basin and West African equatorial forests (Moreau 1966; Kingdon 1990). It further suggests that hybridization driven by these processes predates human influence and that, despite this influence, the current evolutionary status of African elephants may be as fluid as at any point in the past. While the straight lines in evolutionary 'trees', as drawn for elephants by Kingdon (1979) and Roca (2019), among others, unavoidably show abrupt changes between predecessors and successors, the actual process of one species evolving into another is likely to be protracted over epochs. This is what I imagine is happening between these two elephant forms.

I have been drawn into this speculative digression into the relationships between Africa's two extant elephant species by reflecting

on my subjective experience. Historically, the ivory trade distinguished between two quite distinct types of African ivory. Ivory from the rain forest and surrounding areas was referred to as hard and/or yellow, and the tusks were very straight; while ivory from the rest of Africa was soft and/or white and the tusks were curved. As these different qualities affected usage and commercial values, the distinctions were not fanciful but well-established commercial fact. Yet many tusks from countries in and around the Congo basin exhibited features that were intermediate between the two ivory forms and traders had problems deciding which type they were. Parker (1979) refers to such elephants and their tusks as 'cyclotiform' and suggests that such hybrid ivory originates from a far more extensive area than the very limited hybridization zones suggested, for example, by Groves and Grubb (2000). Sources of information on forest elephants mapped by Roca et al. (2019) tend to be peripheral to the equatorial forests, and I suggest relate to cyclotiform or hybrid elephants rather than pure *L. cyclotis*.

The findings presented here raise wider questions about elephantid evolution. It appears that tusks of extant elephants with extreme helical curvature grow to lengths when they no longer function as weapons and tools, other than possibly being used as clubs, as Lister and Bahn (2007) suggested for mammoths, or for display. The extinct genus of *Mammuthus* (but not *Mammot*) shared the extravagantly curved helicoid tusk forms seen in old mature males of both *L. africana* and *E. maximus*. Yet were they also symbols of old age? If male mammoth tusks displayed the excessive curvature that compromised their effectiveness as lethal weapons earlier in life when the animals were in their primes, then this would persuasively support the argument that they evolved for display. This question will only be satisfactorily answered when the tusk shapes and lengths of extinct elephantids are classified by sex and age in suitably large samples. In male savannah elephant, tusks are at their most dangerous when the pair tips are furthest apart, when the animals are in their primes. At this state, tusk lengths are still far short of asymptotes achieved in old age, when elephants are beyond their competitive prime and display would be pointless. I thus concur with Kingdon (1979) and, modifying his words slightly, conclude that "the mature [savannah] male skull [and its curved tusks] are structures adapted to fighting."

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References

- Campbell-Stratton SC, Arnold BJ, Gonçalves D, Granli P, Poole J, Long RA, Pringle RM. 2021. Ivory poaching and the rapid evolution of tusklessness in African elephants. *Science* 374: 483–48.
- Chelliah K and Sukumar R. 2013. The role of tusks, musth and body size in male–male competition among Asian elephants *Elephas maximus*. *Animal Behaviour* 86: 1207–1214.
- Cherney MD, Fisher DC, Auchus RJ. 2023. Testosterone histories from tusks reveal the woolly mammoth's musth episodes. *Nature* 617: 533–539.
- Einstein A. 1931. *Cosmic religion*. Covici-Friede, New York.
- Elder WH. 1970. Morphology of elephant tusks. *Zoologica Africana* 5: 143–159.
- Evans AR, Pollock TI, Cleuren SGC. 2021. A universal power law for modelling the growth and form of teeth, claws, horns, thorns, beaks, and shells. *BMC Biology* 19: 58.
- Fisher DC. 2008. Taphonomy and palaeobiology of the Hyde Park mastodon. In: Almon WD, Nester PL. (Eds.). *Mastodon paleobiology, taphonomy, and paleoenvironment in the late Pleistocene of New York State: studies on the Hyde Park, Chemung, and North Java sites (Palaentographica Americana 61)*. Paleontological Research Institution, Ithaca, pp. 223–272.
- Groves CP and Grubb P. 2000. Do *Loxodonta cyclotis* and *L. africana* interbreed? *Elephant* 2 (4): 8–10.
- Hayden H and Fisher DC. 2011. Coiling geometry of proboscidean tusks. In: *SVP 2011 program and abstracts book*. Society of Vertebrate Paleontology, Deerfield, pp. 123A–124A.
- Hall-Martin AJ. 1987. The role of musth in the reproductive strategy of the African elephant (*Loxodonta africana*). *South African Journal of Science* 83: 616–620.
- Hollister-Smith HJ, Poole JH, Archie E. 2007. Age, musth and paternity success in wild male African elephant, *Loxodonta Africana*. *Animal Behaviour* 74: 287–296.
- Kingdon J. 1979. *East African mammals: an atlas of evolution in Africa. Volume IIIB*. Academic Press. London.
- Kingdon J. 1990. *Island Africa*. Collins, London
- Laws RM. 1966. Age criteria for the African elephant (*Loxodonta africana*). *East African Wildlife Journal* 4: 1–37.
- Lister A and Bahn PG. 2007. *Giants of the Ice Age*. 2nd edn. University of California Press, Berkeley.
- Lister A and Blashford-Snell J. 2000. Exceptional size and form of Asian elephants in western Nepal. *Elephant* 2 (4): 33–36.
- Moreau RE. 1966. *The bird faunas of Africa and its islands*. Academic Press. London.
- Moss CJ and Lee PC. 2011. Female social dynamics: fidelity and flexibility. In: Moss CJ, Croze H, Lee PC. (Eds.). *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 205–233.
- Parker ISC. 1979. The ivory trade. Report to US Fish and Wildlife Service, Washington DC.
- Parker ISC. 2023a. Observations on five savannah elephant clan age structures. *Journal of East African Natural History* 112 (3): 27–39.
- Parker ISC. 2023b. Tusklessness and tusk eruption in the East African savannah elephant. *Journal of East African Natural History* 112 (4): 40–46.
- Parker ISC. 2024a. Further observations on savannah elephant tusks. *Pachyderm* 65: 48–69.

Parker ISC and McCullagh KG. 2021. A compendium of scientific data from 3,169 elephants culled in Uganda (1965–1967), Kenya (1966) and Northern Tanzania (1968; 1969) + data spreadsheet. <https://ufdc.ufl.edu/IR00011446/00001/downloads>

Parker ISC and Graham AD. 2020. Part II. Auctions and export from Mombasa 1960–1978: elephant ivory, rhino horn and hippo teeth. *Pachyderm* 61: 161–175.

Roca AL. 2019. African elephant genetics: enigmas and anomalies. *Journal of Genetics* 98: 83.

Sukumar R, Joshi NV, Krishnamurthy V. 1988. Growth in the Asian elephant. *Proceedings Indian Academy of Science (Animal Science)* 97: 561–571.

Trevor S. 2025. Tsavo: A moment in Time, Chapter 01: <https://f.io/hT27RjvY>; Chapter 02: <https://f.io/zDGhXocu>, Chapter 03: <https://f.io/T9pdVxsn>; Chapter 04: <https://f.io/AuCvf-Ul>; Chapter 05: <https://f.io/7Qckgn-j>; Chapter 06: <https://f.io/YpQybiY4>; Chapter 07: <https://f.io/a60A9DOC>; Chapter 08: <https://f.io/uZjbLOZJ>; Chapter 09: <https://f.io/oOoNpqFv>; Chapter 10: <https://f.io/ISpeStOa>; Chapter 11: <https://f.io/4aGfZOUe>; Chapter 12: <https://f.io/4sA8bkvZ>; Chapter 13: <https://f.io/XR-o166C>; Chapter 14: <https://f.io/vRczK0IF>; Chapter 15: <https://f.io/HXUrCpTj>; Chapter 16: <https://f.io/YX8wvSyk>; Chapter 17: <https://f.io/TV7V2agK>; Chapter 18: <https://f.io/ZCMK5clm>; Chapter 19: <https://f.io/RnNEgByG>; Chapter 20: <https://f.io/RLlrO2jE>; Chapter 21: <https://f.io/6VrUYWgT>; Chapter 22: <https://f.io/P-GGexEV>; Chapter 23: <https://f.io/EIRk-tyy>; Chapter 24: <https://f.io/2HTNMMsZ>; Chapter 25: <https://f.io/xdQiBTPk>; Chapter 26: <https://f.io/tFTAenqQ>; Chapter 27: <https://f.io/yD-OBdoC>; Chapter 28: <https://f.io/lp571CKE>; Chapter 29: <https://f.io/jOogLXNm>; Chapter 30: <https://f.io/1-KLcm8y>; Chapter 31: <https://f.io/zTwJEy2S>; Chapter 32: <https://f.io/oSzrlTh4>; Chapter 33: <https://f.io/IyQnq3G6>; Chapter 34: <https://f.io/vFa2QoOo>; Chapter 35: <https://f.io/3gVSo4i5>; Chapter 36: <https://f.io/EQyNT6Ub>