



Mortality and the magnitude of the “wild effect” in chimpanzee tooth emergence

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ABSTRACT

Age of tooth emergence is a useful measure of the pace of life for primate species, both living and extinct. A recent study combining wild chimpanzees of the Tai Forest, Gombe, and Bossou by Zihlman et al. (2004) suggested that wild chimpanzees erupt teeth much later than captives, bringing into question both comparisons within the hominin fossil record and assessment of chimpanzees. Here, we assess the magnitude of the “wild effect” (the mean difference between captive and wild samples expressed in standard deviation units) in these chimpanzees. Tooth emergence in these wild individuals is late, although at a more moderate level than previously recorded, with a mean delay conservatively estimated at about 1 SD compared to the captive distributions. The effect rises to 1.3 SD if we relax criteria for age estimates. We estimate that the *mandibular* M1 of these wild chimpanzees emerges at about $3\frac{2}{3}$ – $3\frac{3}{4}$ years of age. An important point, often ignored, is that these chimpanzees are largely dead of natural causes, merging the effect of living wild with the effect of early death. Evidence of mortality selection includes, specifically: younger deaths appear to have been more delayed than the older in tooth emergence, more often showed evidence of disease or debilitation, and revealed a higher occurrence of dental anomalies. Notably, delay in tooth emergence for live-captured wild baboons appears lower in magnitude (ca. 0.5 SD) and differs in pattern. Definitive ages of tooth emergence times in *living* wild chimpanzees must be established from the study of *living* animals. The fossil record, of course, consists of many dead juveniles; the present study has implications for how we evaluate them.

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Introduction

Development and eruption of teeth provide a critical window on demography and life history of living and extinct mammal species, whether used to assess single individuals or in species comparisons (Schultz, 1935; Bromage and Dean, 1985; Smith, 1989; Smith et al., 1994; Kelley and Smith, 2003; Dean and Smith, 2009). For primates, perhaps the best-known mammals, tooth emergence is known to be highly correlated with important aspects of life history (Smith, 1989). Great apes are especially important in this regard because, next to humans and elephants, they have the longest absolute time to maturity of any terrestrial mammal¹. The chimpanzee (*Pan*), as our closest living relative, is also our touchstone for

evaluating the evolution of growth and development in the human fossil record. Indeed, our most direct reconstructions of the pace of life histories of *Australopithecus*, *Homo erectus*, and Neanderthals have come by comparing tooth emergence timing with great apes and humans (e.g., Bromage and Dean, 1985; Smith et al., 2007b; Dean and Smith, 2009).

For primates in the wild, most of our knowledge of tooth emergence derives from baboons, where studies of wild-living animals tend to report delays of the premolar/canine complex or third molars compared to captives (Altmann et al., 1981; Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991; see also Dirks et al., 2002). For great apes, however, our knowledge of tooth emergence remains overwhelmingly based on captives (see Smith et al., 1994). And until recently, available observations on wild chimpanzees had not been collected together. Zihlman et al. (2004) made the first synthesis, taking data from living records and natural deaths in wild chimpanzees at Gombe National Park, Tanzania, and at Bossou, Guinea, in combination with chimpanzees of the Tai Forest of Côte d'Ivoire. Their study led them to the firm conclusion that wild chimpanzees show an “unambiguous pattern” of delay:

Emergence of the permanent teeth in wild chimpanzees is consistently later than 90% of the captive individuals. In many

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¹ According to Nowak (1999), initial sexual maturity of females is reached at age 11 years in elephants and at ca. 7 years of age in great apes. Within their respective orders, other mammals attaining this mark late are the grey kangaroo (1.7–3 years), giant anteater (2.5–4 years), North American porcupine (2.5 years?), giraffe (3.5 years), hippo (3–7 years), black rhino (4–6 years) and grizzly bear (4–6 years). Delaying female sexual maturity until 10 years of age is more frequently documented for aquatic mammals, including sirenians and some cetaceans.

cases, emergence times are completely outside the known range recorded for captive chimpanzees (Zihlman et al., 2004: 10541).

The magnitude of the delay was estimated to be so large, they warned, that distinctions would be blurred between wild chimpanzees and *Homo erectus*. Thus, systematic differences between captive and wild populations could add systematic errors to our view of the timing and evolution of life histories. And because teeth are thought to be among the tissues more robust to environmental influences (Dickerson and Widdowson, 1960; Garn et al., 1965), a large delay in tooth emergence has major implications for health assessment of an endangered species. It therefore becomes important to quantify the effect of living in the wild compared to captivity, for understanding both paleontology and neontology of higher primates.

Our purpose here is to measure the “wild effect,” which we define specifically as *the mean difference between captive and wild samples expressed in captive standard deviation units*. To do this, we reexamine wild chimpanzees using a vetted and expanded sample of animals, comparing them to an array of the best captive studies. In constructing the data set, we made all new observations on Taï Forest cases, added new cases (see also Smith et al., 2010), and analyzed data in a manner that eliminates extrapolation to future or past states of tooth emergence. We then added data on whether subjects were living or dead, and asked if morbidity and mortality play roles in dental development. Lastly, we consider if our results are applicable to chimpanzees of contemporary African forests, wild chimpanzees at anytime, or to wild primates in general, including early hominins.

Materials and methods

Vetting the raw data (ID and age)

Wild data here and in Zihlman et al. (2004) largely come from an extraordinary collection of cadavers from the Taï Forest, Côte d'Ivoire, representing a wild population that has been followed for many years (Boesch and Boesch-Achermann, 2000). Great effort has been made to recover skeletons of individuals of known life histories and track causes of death, yet complexities remain. In the wild, unless a death is directly witnessed, an individual just simply disappears. Field personnel identify bodies found in various states of decay, thus identifications cannot be of equal certainty. Moreover, in the Taï Forest, an Ebola epidemic killed many chimpanzees in November of 1992, compounding these difficulties.

The Taï Forest collection is now curated at the Max Planck Institute for Evolutionary Anthropology (MPI EVA) in Leipzig. In order to make our study of this collection replicable and easy to follow, we use individual names and collection numbers preserved at MPI EVA instead of the unique referents (e.g., TF1, GM1, etc.) of Zihlman et al. (2004). The complete data set, including both new and previously studied individuals from Zihlman et al. (2004), now includes a total of 30 cases (see Table 1). Cases are grouped in sets I–III, corresponding to precision of age estimates. For Group I, which includes most of the younger Taï Forest individuals, birth and death dates are usually known.

Taï Females 1 and 3 represent the two key cases (illustrated in Zihlman et al. [2004: Fig. 1] and shown here in Fig. 1). Molars of these individuals were extracted and sectioned to count increments in order to test whether or not their age matched their given identity (see Smith et al., 2010). Taï Female 1 (TF1) refers to ID 11788, which represents a cadaver identified by field workers as the known individual Piment, who died at age 3.76 years. We can confirm Piment's identity through histology because counts of daily bands in her upper first molar indicate a lifespan of 3.82 years

(Smith and Tafforeau, 2008). The older TF3 (11791), however, first thought to be the 8.3-year-old Xindra (Zihlman et al., 2004, 2007), lived to only 6.41 years according to dental histology. Subsequent re-examination of field notes and the skeleton led Smith et al. (2010) to conclude that 11791 is Goshu, a female chimpanzee who was last seen alive at age 6.42 years with severe head and neck wounds from a leopard attack. We suggest that these wounds are consistent with damage observed for specimen 11791. The cadaver was misidentified in the field, we believe, because it was found in the forest in an advanced stage of decomposition in late 1992 during a time of multiple deaths.² Thus, Smith et al. (2010) used an age of death of 6.45 years for Goshu.

Here, as in Zihlman et al. (2004), observations on Taï Forest *Pan troglodytes verus* are augmented with one individual *Pan troglodytes verus* from Bossou, Guinea (Matsuzawa et al., 1990), and several Tanzanian *Pan troglodytes schweinfurthii* specimens from Gombe (see Goodall, 1986). Although we might wish to restrict analysis to a single locale and subspecies, Gombe data fill in critical age groups, especially ages 7–8 years. Gombe data increase heterogeneity even more, however, because they represent a mixed set of observations on the living and the dead. As a case in point, Flint, the famous son of the matriarch Flo (Goodall, 1986), was heavily represented previously by observations stretching over his life and death (GM3 in Zihlman et al., 2004: Table 1). Here, we restrict his input to the more complete data available at his death (Zihlman et al., 1990). Other observations on living Gombe individuals derive from Pusey (1978), who noted if permanent anterior teeth could be seen in free-living juveniles at Gombe, although initial stages of emergence were probably not observable. Among Pusey's subjects, ages are known with enough confidence for present purposes (e.g., observations on Atlas, Goblin, Honey Bee, and Flint). It should be noted that Atlas, Goblin, and Flint died in years subsequent to Pusey's observations.

We especially wish to use all possible information for our few individuals with precisely known ages. In the case of Taï's Goshu (Fig. 1B), left and right sides are asymmetric in emergence: I² is just emerged and slightly stained on the right but not emerged on the left. Rather than choose one side or the other, we ran the analysis twice: once with Goshu's I² scored as erupted and once with it scored as unerupted, reporting the midpoint of the two analyses. In a larger data set it would be preferable to choose a side randomly.

Group II (in Table 1) consists of cases with more substantial approximation involved in age estimates. For several of these cases, birth is known only to the year, although death tends to be known within a month. Because chimpanzees show no seasonality in births (Boesch and Boesch-Achermann, 2000), we assign these cases a mid-year birth date of the first of July, a convention that limits error to ± 6 months. Because Zihlman et al. (2004) did not use this convention, our analysis corrects ages downwards.

Each Group II case marked as approximate (\approx) has a unique story about his or her age estimate. For example, at Taï, Tina's birth year was estimated when she was first seen as an older infant. Michaelmas (1973–1985) from Gombe has a fairly reliable age estimate at least to year (Goodall, 1986). For older juveniles and young adults, the fusion of the basilar suture (the synchondrosis of the basi-occipital and sphenoid at the skull base) acts as a check on age seriation (see Fig. 2). In our sample, Nerone is thought to have been about 13 years of age at the time of his death, but he has no exact birth date; his skull shows all teeth erupted and an open basilar suture. Agathe, at just over 15 years

² The case is fully explicated in Smith et al. (2010). When teeth can be sectioned, age is relatively young, and histology is studied by experts, age of death of great apes has been captured correctly within days or weeks (Schwartz et al., 2006). It is neither practicable nor advisable to use destructive methods to test-match age and identity for all the Taï juveniles at present.

Table 1
Identification, sex, age, cause of death, anomalous teeth, and status of emergence of maxillary permanent teeth plus mandibular canine for wild chimpanzees. Ten new subjects from the Tai Forest have been added since previous study (Zihlman et al., 2004) along with two from Gombe (Pusey, 1978), ordered in three groups by the basis of age assignment.

Site and ID	Assigned identity	Sex and Zihlman et al. (2004) ID ^a	Age (years) ^b	Zihlman et al. (2004) age (years)/ID ^c	Cause of death	Tai dental anomalies ^d	Tooth is unerupted (0) or erupted (1)									
							M ¹	I ¹	I ²	M ²	P ^{3,4}	C ¹ /C ₁	M ³			
Group I. Birth and death dates or histology.																
Tai 13432	Leonardo	TM1	1.77		Starvation		0	0	0	0	0	0	0/0	0		
Tai 11777	Bambou	TM2	2.13		Tree fall		0	0	0	0	0	0	0/0	0		
Tai 11788	Piment	TF1	3.76		Ebola		0	0	0	0	0	0	0/0	0		
Tai 11783	Manon	TF2	5.19		Ebola		1	0	0	0	0	0	0/0	0		
Tai 14995	Oreste	M	5.24		Pneumonia		1	0	0	0	0	0	0/0	0		
Tai 12175	Hector	TM3	5.70		Disease		1	0	0	0	0	0	0/0	0		
Gombe	Atlas	M	6.25		(Living at obs.) ^e	–	1	1								
Tai 15007	Janine	F	6.42		?		1	0	0	0	0	0	0/0	0		
Tai 11791	Goshu	TF3	6.45	8.3 Xindra ^e	Leopard		1	1	1–0 ^f	1	0	0	0/0	0		
Gombe	Goblin	M	7.00		(Living)	–	1	1								
Gombe	Honey Bee	F	7.17		(Living)	–	1	1	1							
Tai 13433	Lefkas	TM4	7.61	8.2	Pneumonia	1	1	1	1	1	0	0/0	0			
Tai 14991	Endora	F	7.96		Pneumonia		1	1	1	0 ^g	0	0/0	0			
Gombe	Flint	GM3	8.50		Starvation	–	1	1	1	1	0	0/0	0			
Tai 15020	Dorry	F	9.98		Anthrax	3	1	1	1	1	1	0 ^h /1	0			
Tai 15021	Gargantua	M	10.16		Anthrax							/0				
Tai 13437	Kana	F	11.40		Leopard	4	1	1	1	1	1	1/1	0			
Group II. Estimated birth month or year.																
Tai 11790	Tina	TF4	≈9.6	10.5	Leopard		1	1	1	1	1	0/1	0			
Gombe	Sherry	GM4	≈10.1		(Living)	–						1/1				
Tai 11776	Ariane	TF5	12.3 ± 0.5		Ebola		1	1	1	1	1	1/1	0			
Tai 11792	Zerlina	TF6	12.3 ± 0.5		Ebola	2	1	1	1	1	1	1/1	0			
Tai 11779	Clyde	TM5	12.6 ± 0.5	13.5	Poacher	1?	1	1	1	1	1	1/1	0			
Gombe	Michaelmas	GM5?	≈12–13	13.0	Wasting	–	1	1	1	1	1	1/1	1			
Tai 15008	Nerone	M	≈13.5		Conspecific attack		1	1	1	1	1	1/1	1			
Gombe	McDee	GM6?	≈13–15	13.4	Polio (euthanized)	–	1	1	1	1	1	1/1	1			
Tai 11775	Agathe	TF7	≈15.4	16.5	Ebola		1	1	1	1	1	1/1	1			
Tai 11903	Fitz	TM6	≈19	14.2 Sartre ⁱ	Ebola		1	1	1	1	1	1/1	1			
Group III. Young plus imprecise.																
Tai 15005	Max	M	6.4 ± 0.5		?		1	0	0	0	0	0/0	0			
Tai 15011	Noah	M	6.6 ± 0.5		Anthrax		1	0	0	0	0	0/0	0			
Bossou	Npei	BM1	≈6.5		Parasites?	–	1	0	0	0	0	0/0	0			

^a Prefixes T(ai), G(ombe), and B(ossou) denote subjects studied by Zihlman et al. (2004).

^b Ages vary in accuracy: ±0.5 denotes birth known to the year only; ≈ denotes birth year and month estimated.

^c If substantially different from age used here.

^d Number of dental anomalies for Tai subjects; Gombe and Bossou were not seen.

^e See Pusey (1978) for observations of living Gombe chimpanzees.

^f The right I² has emerged, the left I² has not (see also Zihlman et al., 2004).

^g Upper second molar seems at point of gingival emergence, but no stain or discernable wear to confirm.

^h Signs of infection near her upper canine (at the edge of emergence) makes Dorry a questionable addition.

ⁱ New DNA and/or histology studies have changed subject identity since Zihlman et al. (2004, 2007).

of age at death, has full fusion of the suture. Our most questionable age is that of McDee (GM6), who died in 1966. Goodall estimated his birth year as 1953, long before she first saw him (see Goodall, 1986). In an earlier study of Gombe skeletal remains, Jurmain (1997) estimated McDee's age as 13–15 years; Zihlman et al. (2007) gave an age of 13.4 years. Given the partial fusion of his basilar suture at death, we use the midpoint of Jurmain's estimate of 14.0 years. Our oldest individual is Tai specimen 11903 (Table 1), or TM6 in Zihlman et al. (2004). The skeleton has been re-identified as Fitz, changing the associated age from 14 years to 19 years, making the case too old to contribute materially to our findings.

There is no question that Group II ages are approximate, with errors of ±1 year when birth and death are listed only to year—more if a birth year is incorrect. Once all teeth are emerged, however, error in age assessment has a diminishing effect on analysis; for these data, as long as the last four cases are indeed older than Michaelmas (ca. 12–13 years), even substantial errors would have minimal consequences for results. On the other hand, for younger cases, error can be critical. Three younger cases have a potential of large proportional error (Table 1, Group III): one case

from the site of Bossou (BM1 in Zihlman et al., 2004), an individual named Npei, who died at ca. age 6.5 years, but was first seen at what was estimated to be 1 year of age. Similarly, in the Tai Forest, Noah and Max died sometime in their seventh year. Npei, Noah, and Max are all “six-year-olds” with upper first molars erupted around a complete deciduous dentition—suggesting a late I¹ if they are 6.0 years of age or a very late I¹ if they are 6.5 years of age. Because precision of their age estimates has a disproportionate effect on results, Group III is discussed separately in subsequent sections.

Even with the best efforts, the data set remains thin; thirty individuals would be fine with longitudinal follows, but with cross-sectional records and a slow-growing species, we cannot encompass all events. And because the sample accumulated largely through natural deaths, we have no choice regarding the age distribution. Thus, we see an abundance of six-year-olds, but only one individual between the ages of 2.5 and 5 years (see Fig. 2). Although Smith et al. (2010) rejected cases with estimated age, here we accept that estimates still contain information, and examine whether or not material is sufficient to sustain Zihlman et al. (2004) and to measure a wild effect.

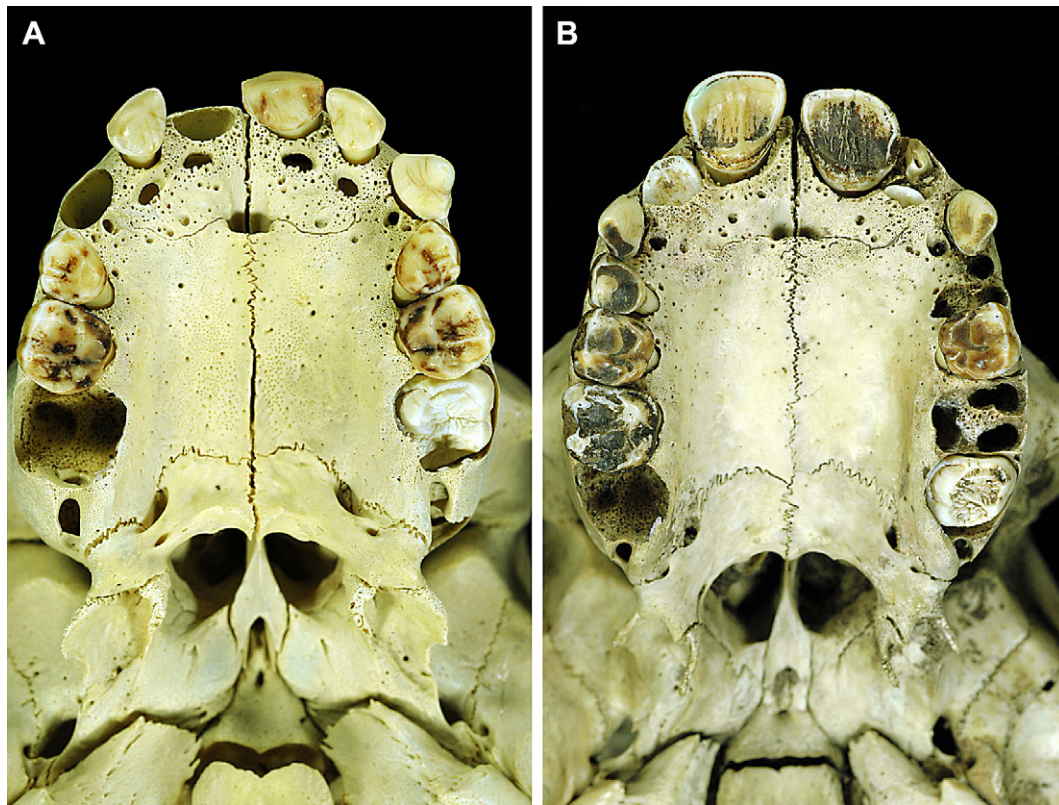


Figure 1. Maxillae of Tai Forest chimpanzees at critical ages, denoted TF1 and TF3 in Zihlman et al. (2004: Fig. 1). Smith et al. (2010) confirmed identity of 11788 (A) as the female Piment, of known age 3.75 years, by close match to dental histology (3.82 years); (B) 11791, previously thought to be Xindra, age 8.3 years, proves to be only 6.41 years of age by histology and has been re-identified as the female Goshu, last seen severely wounded at 6.42 years of age. In (A), upper first permanent molars have not emerged through the gingiva (right M¹ has been removed for study and incisor positions corrected from Zihlman et al. [2004]). In (B), the right, but not the left I² had cut the gingiva; the left M¹ and right M² have been removed for study. Note the wide-open sphenoid-occipital synchondroses (also called the basilar suture) on both.

Tooth emergence

We reexamined and rescored tooth emergence in all cases from the Tai Forest (see Smith et al., 2010). Data for Gombe chimpanzees, including tooth emergence and life histories, are taken from the

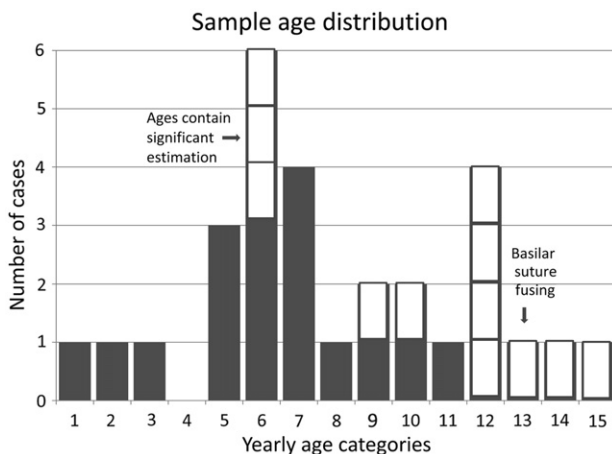


Figure 2. Age distribution of wild chimpanzees in the study sample, combining Tai Forest, Gombe, and Bossou; solid blocks are cases with closely-known age; outline blocks involve approximation of month or year of birth. Note that a critical age group (4-year-olds) is entirely missing and that no exact ages are available past age 11, although fusion of the basilar suture provides one check on estimates. Such strongly-peaked cross-sectional samples are not suited to range calculations or simple averaging to locate onset of developmental markers. The three 6-year-olds of imprecise age have a substantial effect on results.

literature, primarily Pusey (1978), but also Goodall (1986), Jurmain (1997), Zihlman et al. (1990, 2004, 2007), and Williams et al. (2008).

The goal is to match the criterion of emergence standards in studies of living humans: a tooth is scored as emerged when any part of it cuts the gingiva. Emergence status is often clear in dried skull material, but for teeth in the process of erupting, the presence of wear facets and condition of alveolus can be examined; in great apes, teeth quickly pick up a protein stain as they cut (see Kelley and Schwartz, 2010). For teeth near emergence, Zihlman et al. (2004) extrapolated either forward or backward in time to estimate age of gingival emergence. Although this approach is necessary when $N = 1$, when there is a sample—even a tiny sample—of data, standard cross-sectional analysis has advantages (Garn et al., 1958; Smith, 1991a). Simply stated, maturation data have common pitfalls. Whenever subject ages are distributed unevenly or cut-off prematurely—clearly the case for our sample (Fig. 2)—simple calculations of average and midpoint become biased towards the most-represented age, producing “mimicry,” in which summary calculations reflect back the sample age distribution (Bocquet-Appel and Masset, 1982). Moreover, the simple average is particularly subject to *late* bias when subject age is “censored” (i.e., cut-off) at youngest ages, longitudinal data are uncorrected for exam interval, or when birth date is counted from the beginning of the year. Tabulating the age range of subjects who have *already passed the event*, as in Zihlman et al. (2004), will also tend to late bias.

With a standard cross-sectional approach, raw data are simple to layout: each tooth is scored as erupted (1) or unerupted (0) and no suppositions are made as to status in the future or past (Table 1). Observations on living chimpanzees (e.g., Pusey, 1978) become a record of the age a tooth was observed to be present, without

need for extrapolation to initial emergence. In cross-sectional solutions, the age of tooth eruption is recognized as *the age at which 50% of subjects have a tooth emerged*, a quantity that is equivalent to the mean age of tooth emergence observed in properly-corrected longitudinal studies (Carr, 1962). The gold standard is to graph a cumulative frequency curve, solving for the 50th percentile by anything from a hand drawn curve to logistic regression or probit analysis (Cattell, 1928; Kuykendall et al., 1992). The logistic curve fit for the cumulative frequency of emergence of the M² to present data is shown in Fig. 3; the curve intersects the 50th percentile at 7.3 years, representing the median age of emergence of the tooth. Logistic regression is similar to probit analysis, although the latter makes additional assumptions about normality.

Both probit and logit analyses assume that there is variation in the response variable (Garson, 2009); meaning, in our case, sampling should be dense enough to uncover at least one time interval in which between 0% and 100% of cases have erupted the tooth in question. If not, the critical interval is inadequately sampled (see Kuykendall et al., 1992). Because Taï juveniles are more often known from skulls than mandibles, our analysis concentrates on the maxillary teeth; even here, the maxillary canine sample is barely acceptable and the premolar data are clearly insufficient (Zihlman et al. [2004] also dismiss premolars). Complicating analysis of the canine, our one individual on the verge of erupting C¹, Dorry, shows some signs of infection near the tooth; fortunately, the mandibular canine is better represented in the data. A lack of mandibles for Manon, Hector, and Janine (Table 1) leave few data to define eruption of the earlier teeth. Both upper and lower first permanent molars, however, merit discussion because eruption of M₁ has been critical to considerations of the life history of extinct primates (Smith, 1991b; Kelley and Smith, 2003).

Because of uncertainty of some ages, we first grouped subjects to whole years, as in Fig. 3. For a second analysis, we pushed age definition to the limit, entering each individual with his or her most exact age, calculating median age of emergence with binary response logistic regression. For this second analysis we exclude Group III because of the unknown error in age estimates. As will be seen below, analytical choices regarding Group III influence results.

Morbidity and mortality

Causes of death vary (Table 1). In addition to Ebola, other known causes of death in the Taï Forest include: disease (chronic and epidemic), accident, conspecific aggression, predation, and poaching (Boesch, 2008). From Gombe, three of our cases are known from

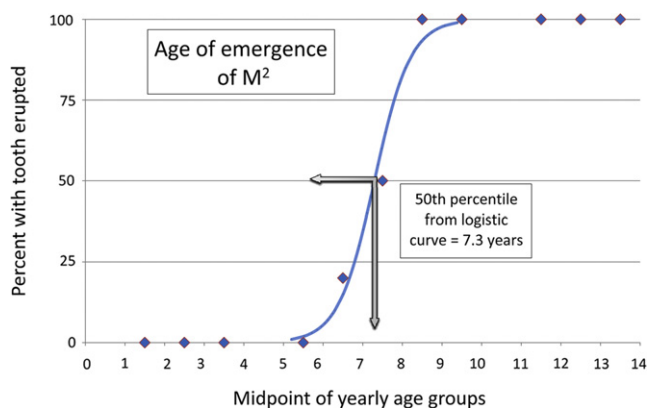


Figure 3. Cross-sectional solution of age of emergence of M² in wild chimpanzees. Cases are grouped by whole year using all data in Table 2 (Groups I–III), plotting the percent with the tooth emerged for each age group. The 50th percentile from the logistic regression is comparable to the mean from longitudinal studies.

autopsy or dried skulls: McDee was euthanized after being severely disabled by polio (Goodall, 1986); Michaelmas, who had recovered from severe hip dislocation when younger, died of wasting (Williams et al., 2008); and Flint, the famous case of the sickly juvenile still dependent on his mother after age 8, died of starvation shortly after his mother died, although contributing factors included peritonitis, gastroenteritis, and a heavy parasite load (Zihlman et al., 1990).

Even a cursory examination of the Taï Forest juveniles reveals malformed teeth, agenesis, peg, and supernumerary teeth. It was important to determine if frequency and severity of anomalies seen in the dead juveniles characterizes the entire Taï Forest collection, especially those who lived long enough to die as adults. Thus, we also surveyed dental anomalies in the larger Taï collection. For this comparison, we classified individuals as juvenile versus adult, using closure of the basilar suture as a marker of adulthood (ubiquitous above age 14 years), excluding cases younger than about 6 years of age, in which little can be seen of permanent teeth. Three new juveniles of unknown identity were examined along with seventeen adults (detailed in SOM Table S1). Of the adults, eight known individuals proved to be 15–29 years old; a further seven cases were of unknown age, but of similar dental wear. Oldest adults, apparently those over 30 years of age, could not be assessed since wear or caries had destroyed the dental morphology if not most of the dentition.

Captive studies

At least three studies of permanent tooth emergence are available for captive chimpanzees (see Table 2). Of these, only that of Nissen and Riesen (1964) was purely longitudinal with observations continuing to dental maturity. Their classic study followed 15 male and female chimpanzees from birth at the Yerkes Primate Center through maturation. Young subjects were examined frequently so as to determine age of tooth emergence within a month, something accomplished with little difficulty for many years. But, as subjects began to mature in age and strength, some could only be examined when under periodic anesthesia are undertaken for comprehensive growth studies. Because of the manner in which the study compensated for increasing exam intervals, Nissen and Riesen (1964) cautioned that ranges could be underestimated.

Much later, at a semi-natural enclosure at Stanford, Kraemer et al. (1982) studied a mixed-age sample of 8 males and 9 females for a three-year period to produce a “mixed-longitudinal study.” Data were appropriately corrected for exam intervals. Central tendencies were calculated as the midpoint of *youngest record with the tooth erupted* and *oldest record with the tooth unerupted* (see also Phillips-Conroy and Jolly, 1988). Interestingly, even with a modest sample size, this study produced results quite similar to Nissen and Riesen (1964), even increasing the range slightly for the last-erupting M³, extending it up to age 14.

The third study is a large mixed-longitudinal study of 22 male and 36 female chimpanzees born at the Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP) in New York, where subjects were enrolled at different ages and followed for varying time intervals (most between 3 and 7 years), with no observations beyond age ten (Conroy and Mahoney, 1991). Data regarding first molars are well represented in the LEMSIP data, but sample size drops off sharply after about age 7.0 years. Zihlman et al. (2004) characterized captive chimpanzees with the early version of the LEMSIP analysis (Conroy and Mahoney, 1991) where estimates are more affected by heavy sampling of young individuals. Kuykendall et al. (1992) later reanalyzed these data with probit analysis. Even with improved data analysis, data censoring limited findings: at the end of the study, no subjects had erupted

Table 2

Central tendency and dispersion of age of permanent tooth emergence (years) gathered from the three major studies of captive chimpanzees.

	Yerkes		Stanford		Both		Lemsip			Captives overall	
	Nissen and Riesen (1964)		Kraemer et al. (1982)		Yerkes-Stanford combined		Kuykendall et al. (1992)				
	Mean		Midpoint		ranges		Median	SD ^a	Range ^b	Grand mean	CV ^c
Maxilla											
M ¹	3.33		3.67		2.75–4.00		3.18	0.37	2.26–4.38	3.39	10.9
I ¹	5.62		5.25		4.50–6.75		5.55	0.51		5.47	9.5
I ²	6.73		6.17		5.80–8.25		6.22	0.60		6.38	9.4
M ²	6.79		6.17		5.67–7.83		6.74	0.67		6.39	10.8
P ³	6.95		6.25		5.83–8.17		6.67	1.05		6.62	15.8
P ⁴	7.35		6.50		6.25–8.33		6.48	0.96		6.80	14.1
C ¹	9.00		7.92		7.42–10.08		8.11	1.07		8.34	12.8
M ³	11.35		12.25		9.75–14.00		–	(1.16)	–	11.80	9.8
Mandible											
M ₁	3.26		3.08		2.67–3.75		3.15	0.55?	2.14–3.99	3.16	10.2
C ₁	8.98		7.92		7.92–10.08		7.88	1.19		8.26	14.4
Average CV										11.8	

^a Standard deviations (SD) from Kuykendall et al. (1992), except M³ (Kraemer et al., 1982).

^b Because LEMSIP is heavily weighted toward very young animals, M1 is the only tooth for which the study expanded both ends of the known range; ranges for other teeth heavily sample the low, but not the high end. Kuykendall et al. (1992) were well aware of the difficulties of these censored data.

^c Coefficient of variation (CV): (Grand mean/SD) × 100.

third molars and only 3.5% had erupted canines. In sum, all captive studies have few data at later ages of maturation (10–14 years), but accurate age assignment.

Results

Range and central tendency

Our three selected studies of captive chimpanzees provide measures of both central tendencies and dispersion for ages of tooth emergence (Table 2). In general, Nissen and Riesen (1964) tended to later ages, Kraemer et al. (1982) to younger, with ages from Kuykendall et al. (1992) in the middle. For third molars, where the LEMSIP sample (Kuykendall et al., 1992) drops out, the other two studies compensate. Because all three studies have strengths, we calculate the grand mean of the central tendencies of the three to represent overall age of tooth emergence in captive chimpanzees. As expected, the coefficient of variation (CV) stabilizes dispersion to near 10, slightly more for some dimorphic tooth positions.

Previous findings of Zihlman et al. (2004) are expressed as a “wild effect” in Table 3. When expressed as the deviation from captives in Z-score units (Z), the magnitude of the delay is inconsistent, varying between <1 Z and nearly 4 Z (note that “a delay of 1 Z” is used throughout as the equivalent of “a Z-score of –1”).

Table 3

Ages of tooth emergence of wild chimpanzees determined by Zihlman et al. (2004) in order of appearance and the magnitude of the “wild effect” implied by their results.

Maxillary tooth	Age of emergence in years from Zihlman et al. (2004)		“Wild effect” ^a
	Range	Central tendency (range midpoint)	
M ¹	4.10	4.10	–1.91
I ¹	6.3–8.4	7.35	–3.69
I ²	7.4–8.6	8.10	–2.87
M ²	8.2–8.4	8.30	–2.85
C	10.1–10.8	10.35	–1.88
M ³	12.40	12.40	–0.51
Average “Wild effect”			–2.29

^a Measured as (Central tendency_{captive} – Central tendency_{wild})/SD_{captive}.

Further, when teeth are listed in order of emergence, there is a steep, fairly ordered decline in the wild effect from high to low, and from early- to late-erupting teeth. Thus, the wild effect cannot be characterized with any one value, although the mean is quite large, at –2.29 SD.

New estimates of tooth emergence in wild chimpanzees appear in Table 4, both in years of age and as the Z-score from the captive grand mean. Results are presented for the total sample (using logistic regression of age groups of yearly intervals) and after excluding Group III, the three “six-year-olds” of inexact age (using binary logistic regression of precise ages). For the total sample, teeth erupt at approximately –1 Z to as much as –2.4 Z compared to captives, averaging –1.3 Z. Disallowing Group III, however, moderates the amplitude of the wild effect considerably, tightening its range to –0.4–1.6 Z with a mean of –1.1 Z. Comparing our results (Table 4) to those of Zihlman et al. (our Table 3), we estimate a lower magnitude for the wild effect across the dentition with the exception of the third molars, where the wild effect is always low.

Table 4

Age of emergence of permanent teeth of wild chimpanzees of Tai/Gombe/Bossou Forests as determined by logistic regression and the magnitude of the “wild effect,” calculated for the subset with more closely determined ages (I–II) and for the total sample (I–III).

	Wild median age of emergence (years)		Captive grand mean/SD	“Wild effect” Z-score ^b	
	Subset I–II ^a	Total I–III		Subset I–II	Total I–III
Maxilla					
(M ¹) ^c	>3.75	>3.75	3.39/0.37	<–0.97	<–0.97
I ¹	6.24	6.70	5.47/0.51	–1.51	–2.41
I ²	6.63	7.06	6.38/0.60	–0.42	–1.13
M ²	7.16	7.30	6.39/0.67	–1.15	–1.36
(C)	10.04	10.14	8.34/1.07	–1.59	–1.68
M ³	12.63	12.94	11.80/1.16	–0.72	–0.98
Mandible					
(M ₁)	<3.75	<3.75	3.16/0.55	>–1.07	>–1.07
C	9.52	9.45	8.26/1.19	–1.06	–1.00
Average “Wild effect”				–1.06	–1.33

^a Table 1 defines subset I–II and total sample (I–III).

^b “Wild effect” measures the shift in central tendency of wild subjects from the captive grand mean in captive standard deviations.

^c Parentheses mark inadequate underlying samples.

With new analysis, the structure/order in the sequence of Z-scores is much less marked than in Zihlman et al. (2004).

Zihlman et al.'s previous study, as quoted above, described captive-wild differences in terms of range, not standard deviations. Although range *per se* is not observable in our cross-sectional sample, we can compare central tendencies calculated here to captive ranges (Fig. 4). Our ranges for captives are somewhat larger than those Zihlman et al. (2004) employ because we include more studies, two of which better sample the later-emerging teeth. When teeth are listed in order of appearance (Fig. 4) range bars should increase toward later-erupting teeth if data are adequate, because dispersion depends on the mean in growth data. Simply looking over the captive ranges, at the very least, ranges of M² and canines appear to be underrepresented.

Leaving aside M¹ for the moment, it is apparent that medians for wild chimpanzees fall within captive ranges, meaning that $\geq 50\%$ of wild and captive cases are expected to overlap in comparable longitudinal studies (Fig. 4). Indeed, in several cases, captive ranges easily encompass wild medians. This holds either for the total sample (thick bar) or for the sample deploying stricter age requirements (i.e., that use only Groups I and II [thin bar]).

Also in Fig. 4, open circles mark central tendency of ranges reported previously by Zihlman et al. (2004). Compared to that study, new results pull I¹, I², and M² eruption firmly into the range of captive subjects, at least into the latter half of captive ranges. For these three teeth, we can attribute slightly more than half the change from Zihlman et al. (2004) to the single factor of correcting the age of TF3/11791 from 8.3 years to 6.4 years. The remaining

effect, however, represents a consequence of a combination of new methodology and new cases. Correcting the age of this young juvenile has minimal effects on estimates for later-erupting teeth. The difference in estimates at the third molar (thick and thin bars) can be attributed to the use of slightly different analyses for grouped versus ungrouped ages; neither estimate differs much from Zihlman et al. (2004).

The first permanent molar: maxilla versus mandible

For M¹ we have no new cases, only that of 11788 (Piment), the 3.76 year-old female whose maxillary M1 had not emerged, described previously by Zihlman et al. (2004). That study extrapolated into the future to predict that Piment's M¹ would have emerged at 4.1 years of age, at the high end of the captive range (maximum of 4.38 years). Instead of extrapolating, we note that her M¹ is delayed by ≥ 0.97 Z relative to captives. Piment's mandible, however, which preserves the alveolus of M₁ (the tooth was not recovered) shows that the root had developed past the cleft stage to a length of 7 mm; Smith et al. (2010) who analyzed the mandible, concluded that mandibular M1 was emerged. If so, M₁ emergence was late by ≤ 1.07 Z.

Morbidity and mortality

In our particular sample of Tai Forest juveniles, the 1992 Ebola epidemic killed across all but the youngest ages (Table 5). Sudden deaths (poaching, leopard attack, and conspecific attacks), on the

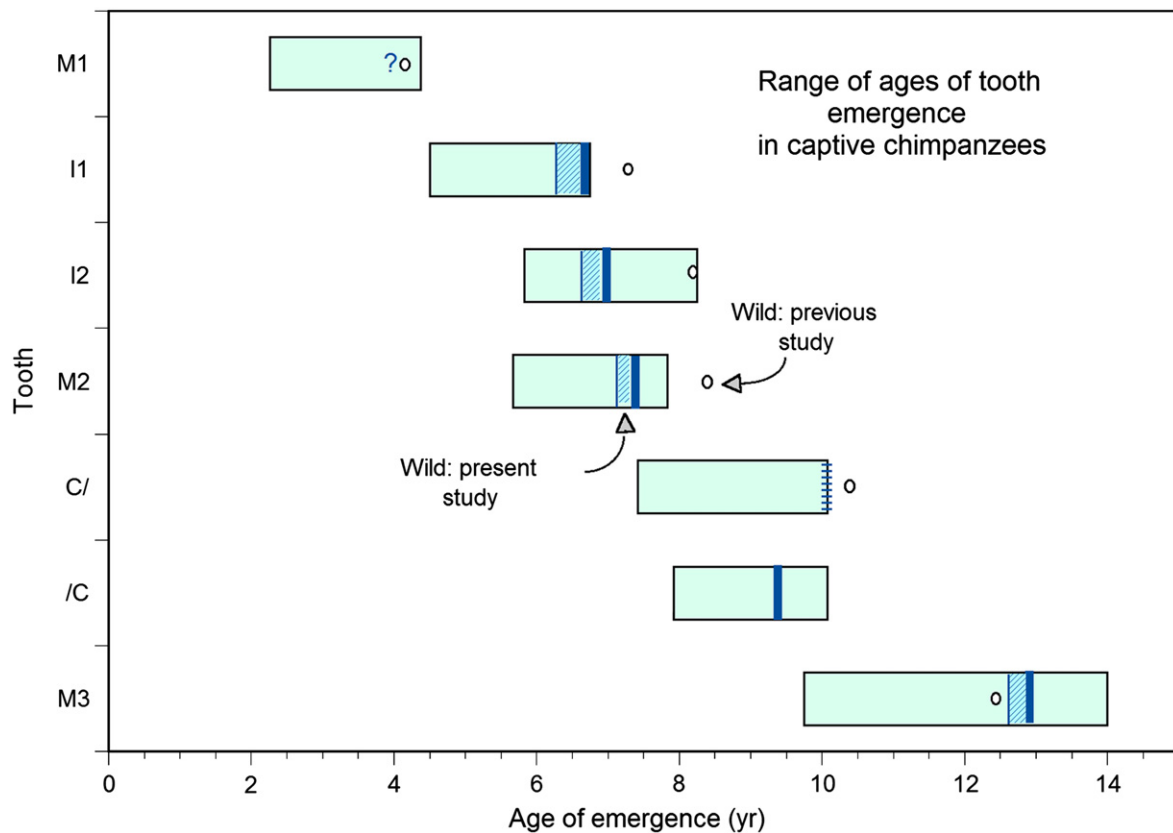


Figure 4. Age of emergence of the maxillary teeth of wild chimpanzees (dark blue vertical bars) compared to ranges reported for captives (shaded light blue); the mandibular canine is added because the maxillary canine (broken bar) remains poorly sampled. Solutions vary slightly by strict (thin bar) or relaxed (thick bar) criteria for age estimates, linked here by diagonal hatching. Open circles plot the range centroid from the previous study of Zihlman et al. (2004). Whether age requirements are strict or lax, new analysis shifts wild means well into captive ranges. No new data are available for maxillary M¹, where $N = 1$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 5

Deaths by age group and debility for wild chimpanzees in the present study (Groups I–III).

Cause of death	Age categories (years) ^a			Total
	1–9	9–15	15+	
Sudden/ accident ^b	2	4		6
Epidemic disease (Anthrax/Ebola/Polio)	3	5	2	10
Debility/disease ^c	7	1		8
Death by unknown cause	2			2
Total observed dead	14	10	2	26
(Total observed alive)	(3)	(1)		(4)
Study total	17	11	2	30
Minimum percent of sample dying of debility or disease	41%	9%	0%	27%

^a Age categories are closed left, i.e., 1.0–8.99 years.^b Includes tree fall, leopard, poacher, conspecific attack.^c Includes non-epidemic diseases and debilitating conditions (pneumonia, parasitization, wasting, starvation).

other hand, fall mainly between ages 9 and 15 years. More debilitating conditions such as pneumonia peak between 6 and 9 years of age in the present data, while starvation was present among both infants (Leonardo) and juveniles (Flint) following the loss of their mothers.

In the study sample, four juveniles showed gross dental anomalies: Lefkas (supernumerary tooth), Kana (multiple agenesis) (Fig. 5), Zerlina (peg teeth and agenesis), and Gargantua (grossly malformed teeth). We find that the heavy proportion of dental anomalies in juvenile deaths (35%) is not repeated in the adult deaths (11%) (Table 6). In fact, the conditions found in the adult group were milder or different: one minor central defect and

Table 6Association of post-canine^a dental anomalies (malformed teeth, agenesis, peg, and supernumerary teeth) with younger deaths in larger Tai Forest skeletal collection.^b

	Juvenile deaths	Adult deaths	Total
	Basilar suture open to initial fusing age ≈6–14 years	Basilar suture fused age ≈15–30 years	
Anomalies by individual			
Absent	11	17	27
Present	6	2	9
Total	17	19	36
Percent of cases with anomalies	35%	11%	25%
Anomalies by total teeth P3–M3 ^c			
Absent	172	349	684
Present	17	3	20
Total	189	352	704
Percent of anomalous teeth P3–M3	9%	1%	3%

^a Incisors and canines are often lost or worn and rarely anomalous.^b Sixteen cases from Table 2 (aged 6–19 years) are combined with 3 new juveniles and 17 new adults known mainly to age category (see SOM Table S1), all from Tai.^c Age category and presence of anomalies are associated by individuals at $p < 0.035$ (one-sided), but expected frequencies are low for reliable p -values; they are highly associated by tooth: $p < 0.001$ by tooth in Chi-squared tests for independence.

one case of hypoplastic malformation (more information in SOM Table S1). In any case, counted by tooth, the juveniles show 9 times the percentage of dental anomalies as the adults. Some juvenile anomalies seem to be major (e.g., Fig. 5B).

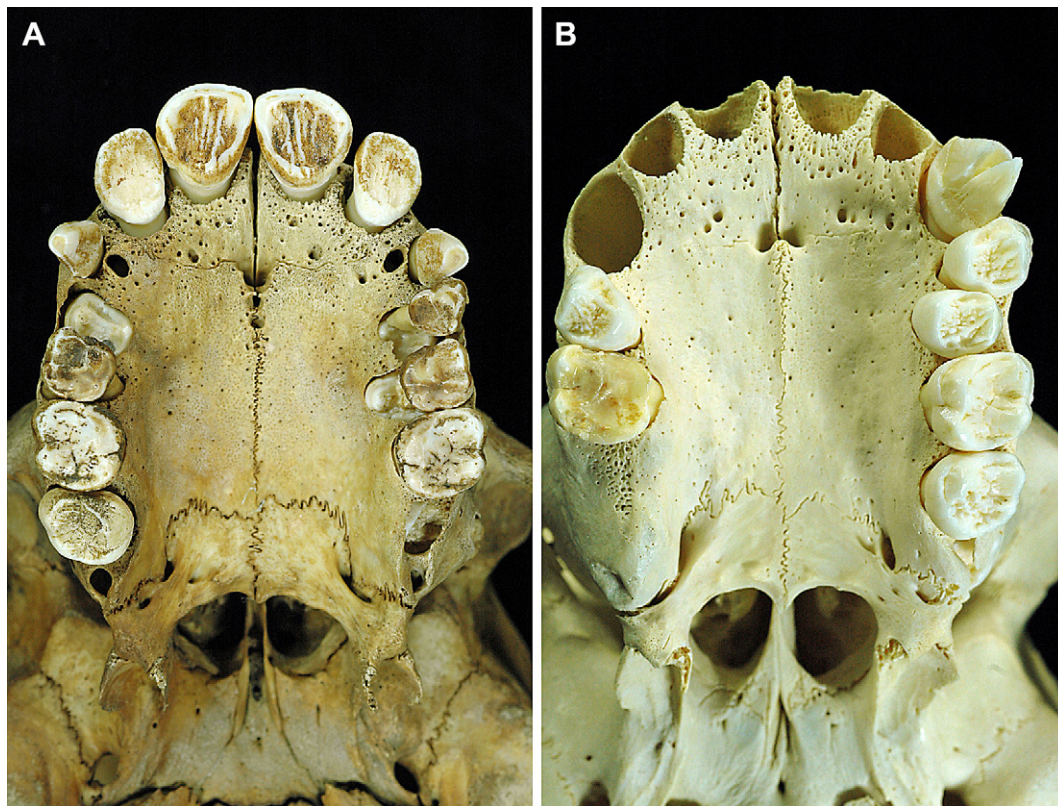


Figure 5. Older juveniles from the Tai Forest with dental anomalies: (A) 13433 (Lefkas), a male aged 7.6 years with mixed dentition, has a supernumerary left molar (or “M⁴ⁿ”) which has impacted M²; (B) 13437 (Kana), a female aged 11.4 years, has apparent agenesis of right P⁴ and M²–M³; a radiograph shows no sign of unerupted teeth and there is no wear facet distal to M¹, which shows heavy wear.

Discussion

Our reanalyses of tooth eruption in wild chimpanzees of Taï, Gombe, and Bossou find some delay in wild compared to captive subjects, but with ranges that must overlap extensively. Differences from a previous study (Zihlman et al., 2004) result from the combined effects of correcting field identification, minimizing error in age estimates, applying cross-sectional analysis, adding new data, and expanding range data for captives (in no cases did these studies disagree about tooth emergence status). The fact that the resulting wild effect is more consistent over the dentition (spanning half the Z-units of the previous report) supports the new approach. The most conservative estimate of the magnitude of the wild effect is a late shift of about 1 SD compared to the captive distribution, as observed with stricter age criteria. The most difficult problem to resolve is whether the larger effect at I¹ in the total sample group is real, a sampling effect, or the effect of slightly overestimated ages of the three six-year-olds of imprecise age (Group III).

Even grouping cases by whole year of age, logistic regression cannot eliminate the influence of uneven age groups. If our sample represents all six-year-olds (e.g., 6.0–6.99 years of age) with subjects ranging only between 6.0 and 6.4 years of age, we will overestimate ages of emergence and the wild effect. At present, our only check on ages of Group III (Max, Noah, and Npei) is to seriate maturation of animals in the group. Thus, according to the amount of I¹ root developed, Goshu (age 6.4 years) is the most mature, declining slightly to Max, and then to Janine (also aged 6.4 years) and Npei (Matsuzawa et al., 1990), with Noah the least developed. Certainly we have variation at age 6.4 years, but no assurance that any member of Group III is actually as old as 6.5 years. Doubts notwithstanding, it does not seem correct to exclude Group III entirely, because they represent a set that failed to make a healthy transition to independent-feeding juveniles. Taking them into account with a total sample, we estimate a wild effect averaging -1.3 Z.

Importantly, our reanalysis does ultimately concur with Zihlman et al. (2004) in that these wild chimpanzees experience later tooth emergence than captives, a result consistent with later attainment of sexual maturity and adult body size (Pusey, 1978; Kimura and Hamada, 1996). As Zihlman et al. (2007) pointed out, wild-living chimpanzees face higher energy costs than captives for locomotion, feeding, and social activities, leaving less energy available for physical growth. Parasite loads must also influence nutritional status. Slower growth and development is also observed in wild-living baboons (Altmann et al., 1981; Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991). A major point that has been overlooked, however, for our particular subjects, is that they are not only wild—they are wild, but sometimes debilitated and obviously now *dead*. They thus represent a special group of mortality-selected individuals without “peers” measured in available captive studies.

“Mortality selection” concerns the non-randomness of death; it is recognized when age cohorts in a population or death assemblage differ, ideally in genotype, but also in phenotype (Lande and Arnold, 1983). Many examples are known for humans and other animals, from higher morbidity and mortality in small-for-date births in contemporary humans, to higher morbidity in younger deaths in cemetery samples (see Humphrey and King, 2000, for review). The problem of making inference to the living, healthy population from a death assemblage, or “the osteological paradox,” has been the subject of considerable attention in bioarchaeology (Wood et al., 1992; Wright and Yoder, 2003).

These chimpanzees merge the effects of wild living with the condition of early death, and present data that do not permit us to disentangle these effects. Evidence suggests, however, that the correlates of early death are not trivial in terms of development. In

chimpanzees, as in humans (see Peden et al., 2008) each age group has its likeliest cause of morbidity and mortality (Hill et al., 2001; Boesch, 2008; Williams et al., 2008). In these chimpanzees, the younger cases critical to determinations of tooth emergence, represent individuals who died of disease or infirmity. On the other hand, older animals often died as a result of extrinsic factors, often including predation or accident (see Table 5). The most debilitated are those under 9 years of age, for which at least 7/17 succumbed to conditions such as parasitization, starvation, and pneumonia. Of particular note, some cases in this important age group have been described as smaller than their age mates, especially Flint (Zihlman et al. [1990] observed that his bone density seemed low) and Npei (Matsuzawa et al., 1990). If we look at the permanent teeth that emerge from 3 to 9 years, M¹-I¹-I²-M², the delay in tooth emergence averages -1.47 Z. Yet at C₁ and M³ emergence, where our sample tends towards accidental death rather than debilitation, the “wild effect” drops to -0.99 Z. For these later-emerging teeth, age estimation would have to be seriously off (underestimated by about 2 years) to produce a major wild effect.

A second sign of morbidity is observable in skulls and dentitions retrieved from the Taï Forest. Specifically, these display a remarkably high number of dental anomalies, some of a severe manifestation (Fig. 5B). Anomalies of number and form are significantly higher in frequency in Taï juvenile deaths compared to adult deaths. As synthesized by Brook (2009), dental anomalies are phenotypes of multifactorial etiology. They may be products of genetic predisposition, genetic modifiers, and epigenetic effects from the specific (e.g., demethylase), but also range to more general factors such as maternal effects (e.g., hormonal in utero), environmental modifiers (e.g., nutrition), and environmental challenges (e.g., infection, trauma, pollutants, etc.). Factors associated with dental anomalies include prematurity, low birth weight, severe malnutrition, neonatal hypocalcaemia, vitamin D deficiency, hormone disturbances, and severe infections, or some combination of these and other problems (Brook, 2009). A high presence of anomalies suggests a group under some pressures in early life; indeed, we might conclude that dental anomalies are a risk factor for illness and death.

Overall, the effect of living wild and the effect of early death sum to a delay of $1-1.3$ Z in tooth emergence in this pool of chimpanzees. If naturally-dead wild chimpanzees lag in tooth eruption to this degree, we might reasonably predict that *living* wild chimpanzees will lag to a lesser degree, somewhere between 0 Z (set as the captive mean) and 1 Z.

Other wild or poor environments

To gauge the significance of a 1 Z lag in tooth emergence, we can compare these chimpanzees to what we know of other mammals in wild or poor environments. Relative delay in tooth emergence of these chimpanzees is compared with two other catarrhines and one generalized mammal in Fig. 6. The first case, by Garn et al. (1973), shows the effect of poverty on tooth emergence as determined in the American Ten State Nutritional Survey, with samples in the thousands. These American children were at poverty level, with an income/needs ratio of 1.0 (i.e., there is no affordable disposable income), a poverty level not particularly extreme in terms of world-wide poverty. Garn et al. consistently found that low income boys, in particular, erupt teeth later than boys of median income, lagging as much as 0.17 SD units in black males, the most affected group (shown here). Because families can move in and out of poverty, some of those children might have been poor too briefly to affect global tooth development, and this may be why the last tooth to erupt (M₂ in these data) showed no effect. The effect on girls was even more moderate.

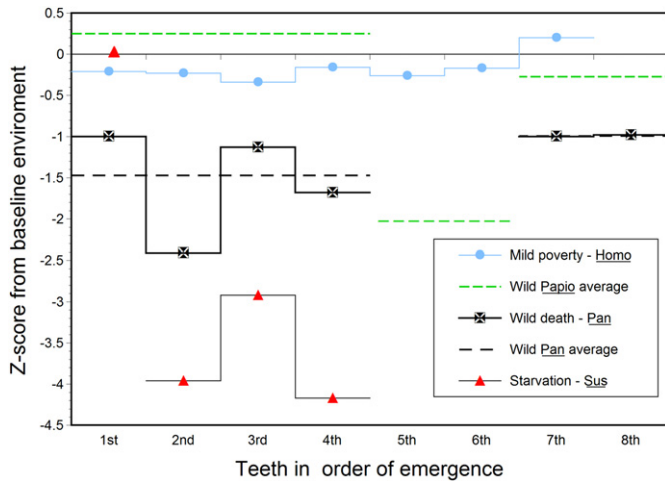


Figure 6. Magnitude of effect of four wild or poor environments on tooth emergence in catarrhines and a generalized mammal. The Z-score from baseline environment plotted for permanent teeth in order of emergence from first to eighth. For human males, mild poverty delayed teeth by an average of 0.17 Z (Garn et al., 1973). Living, wild-captured olive baboons are estimated to have a moderate deviation from captives that manifests mainly in later replacement teeth (premolars). For (primarily) natural deaths of wild chimpanzees, teeth appear delayed more in younger deaths (dashed lines/arrows locate averages at -1.47 Z) versus later deaths (-0.99 Z). Experimental starvation of domestic pigs (extending from 1 month to 1 year of age) produced an extreme effect (McCance et al., 1961): the M1s, largely formed when starvation began, were unaffected ($Z = 0$), but eruption of subsequent permanent teeth (p^1 , I^3 , M^2) was delayed by ca. 3.7 Z. Note resemblance of shapes of *Pan* and *Sus* curves.

The second comparison comes from wild olive baboons (*Papio hamadryas anubis*). Kahumbu and Eley (1991) recorded tooth emergence status when a long-studied wild troop was captured for transfer to a new range. Here, we compare them to captive yellow baboons (*Papio hamadryas cynocephalus*) from Reed in Phillips-Conroy and Jolly (1988). Because dispersion had to be estimated³ (calculations are detailed in SOM Table S2) and because samples are limited for ages 3–6 years, deviations from captives are averaged over sets of teeth (Fig. 6). As Kahumbu and Eley (1991) described, live-captured wild *Papio* are quite similar to captives at the first few maxillary teeth to emerge. The last-emerging C^1 and M^3 were noticeably late, although scaled for standard deviations, the effect is fairly minor. The pronounced lateness of maxillary premolars might be dismissed as sampling error (indeed there are few animals in the critical age range), except that Phillips-Conroy and Jolly (1988) found the same pattern in wild yellow baboons, males particularly. But because premolars erupt 5th and 6th in sequence, they must emerge into a closed permanent tooth row bounded by M1 and a sizable (erupting or erupted) canine, and it is plausible they might be more limited than other teeth by space available in a growing face. In any case, the overall wild effect for living olive baboons is estimated at -0.45 Z. Notably, it takes on a different, even opposite, pattern across the dentition compared to these chimpanzees. And although we had to estimate dispersion for baboons, the typical primate CV would have to be cut in half (e.g., reduced from 10 to 5) to achieve a wild effect in baboons comparable to that observed in these chimpanzees.

³ Coefficients of variation center around 10 for age of tooth emergence across a broad array of well-studied primates (Smith et al., 1994). Standard deviations for captive baboons were estimated by setting CV to 10, allowing a rise to 14 for dimorphic tooth positions in mixed-sex samples, as in chimpanzees (see SOM Table S2). For pigs, CVs were set to 10, but for events within the first year of life, gestation length was added to age before calculating standard deviations.

For an extreme effect, we move to experimental studies. A classic series of experiments by McCance et al. (McCance et al., 1961, 1968; Tonge and McCance, 1965, 1973) investigated tooth development in starved domestic pigs. Born after a normal gestation, 1-month-old pigs were starved to a degree that kept them alive but prevented them from gaining weight; at 1 year of age they had severe marasmus and weighed only 3.5% of control weight (5.5 kg rather than 150 kg!) — a situation that probably could not persist in the wild, where mammals must be strong enough to forage for food. Starvation had extreme consequences for bone growth: by 15 months of age, starved pigs attained only half the skull length of normal controls. Teeth were differentially affected. For example, eruption of the first permanent molar, which formed partly before starvation commenced, seemed unaffected. Eruption of the next three teeth (p^1 , I^3 , and M^2) however, was delayed by months. We must do some estimating again,³ but it appears that starvation delayed M^2 eruption by something near 3.5 Z. Notably, formation of tooth crowns progressed more normally than emergence, which McCance et al. (Tonge and McCance, 1973) proposed was due to tooth crowding in the underdeveloped jaws. This critical series of experiments established a functional explanation for retarded tooth emergence in undernutrition, although more subtle or particular conditions may also retard tooth emergence (see Boughner and Dean, 2004; Brook, 2009; Smith et al., 2010).

In sum (Fig. 6), we can bracket our wild chimpanzee deaths below children living in moderate poverty (-0.17 Z) and apparently below living wild Kenyan baboons (-0.45 Z). Natural deaths in wild chimpanzees, in comparison, come in at -1 Z to -1.3 Z, whereas experimental starvation has a devastating effect on growth and development of pigs (-3.7 Z). Although never as extreme as the McCance studies, diminished facial growth may contribute to the retardation of tooth emergence observed in chimpanzees.

Inference

The question at the heart of the matter can be stated as: is our estimate of the delay in tooth emergence a measure of health and disease in the contemporary African forest or is it widely applicable to wild chimpanzees or wild primates? As suggested by the stepped delays of mammals in four circumstances (mild poverty, life in the wild, wild death, experimental starvation) *there is no one poor environment*; similarly, *there is no one wild environment*. These chimpanzees, for example, died in the contemporary African Forest, a forest which may have fewer predators but more epidemic disease than in the past (Leendertz et al., 2004). Moreover, among wild chimpanzees, mortality is higher in the Tai Forest than at Gombe or Mahale (Hill et al., 2001). More delayed development in the younger deaths and a heavy burden of dental anomalies in juveniles as a whole give evidence of mortality selection consequent to developmental stress, frailty, or both stress and frailty (see Møller, 1997; Wright and Yoder, 2003; Brook, 2009), suggesting that these individuals were disadvantaged in ways that were longstanding and that ultimately influenced survival (King and Ulijaszek, 1999).

If we wish to know the age of tooth emergence in living wild chimpanzees, however, we will have to study *living* animals. And although we have some data on growth and development of living wild chimpanzees we necessarily have sparse coverage of the dentition (Pusey, 1978). Solving this problem may not warrant interfering with a highly endangered species, yet, on the other hand, the present data show that we can estimate age of tooth emergence with fewer data than one might think. And, although it will take time and resources, histological study of collections wild shot in the 19th and 20th centuries could provide data more comparable to living wild subjects (e.g., Kelley and Schwartz, 2010).

If we solve the problem of age of tooth emergence in living wild and in wild-shot chimpanzees, we can provide age assessment for any number of scientific studies of this endangered species.

Since Zihlman et al. (2004), discussions are beginning to adopt 4.0 years as the age that wild chimpanzees erupt first permanent molars (Gibbons, 2008; Kelley and Schwartz, 2009). Although this is an appealing round number, it ignores the lag of upper to lower molars (see Table 3), which can be substantial. Indeed, equations relating life history to age of first molar eruption are based on *mandibular* M1 (Smith et al., 1994), a tooth which erupts earlier than its maxillary counterpart (see Table 3). If we use the conservative estimate of a delay of about 1 Z suggested by the present study, rather than only the individual Piment (above in Fig. 1), we arrive at an estimate for emergence of M₁ at ca. $3\frac{2}{3}$ – $3\frac{3}{4}$ years and M¹ at $3\frac{3}{4}$ years (Smith et al., 2010). Whether or not this is any better than determinations based on $N = 1$, awaits further evidence (see Kelley and Schwartz, 2010).

The fossil record

The pointed question for paleontology focuses on how much these findings apply to the fossil record—after all, the fossils are all dead. Here, we would argue that particular conditions of morbidity and mortality may be critical. Whenever we deal with dead juveniles, we must take note of their source: are they wild shot, deaths from debility, or deaths from predation or accident? Did the individual die at, or live through, the event of interest (see Wright and Yoder, 2003)?

At least two outside sources of information can come into play: taphonomy and pathology. For example, concentrations of infants and young juveniles accumulated by predators, such as the Swartkrans cave (Brain, 1981) may well be a healthier class than the intentional child burials of the Middle Paleolithic. Other indications of pathology are also critical, a point made by the experimental studies of McCance and colleagues. When teeth of starved pigs were sectioned, they were found to show major pathologies of fine structure in addition to grossly observable malocclusion, impactions, and anomalies (McCance et al., 1968). This is a reminder that real debility leaves signs on teeth and bone. Anytime we study teeth of individuals who died young, we need to be aware of signs of morbidity (e.g., enamel hypoplasias, dental anomalies). The death assemblage of wild chimpanzees studied here serves as a cautionary tale, but given their heavy burden of dental anomalies and death by disease, it is not clear they comprise an across-the-board model for all early deaths in the hominin fossil record.

We now have at our disposal techniques that, by aging individual deaths in the fossil record, promise to lay open the evolution of mammalian growth and development (Bromage and Dean, 1985; Beynon et al., 1998; Dean et al., 2001; Kelley and Smith, 2003; Smith et al., 2007a; Smith and Tafforeau, 2008; Dean and Smith, 2009; Dirks et al., 2009). As our sample of known age individuals from extinct species increases, we can begin to consider the influence of mortality selection, taphonomy, and pathology as we try to sort out what was typical for healthy individuals in the past. The living chimpanzees of the Taï Forest, we expect and hope, are on a better course than the young juvenile deaths described here.

Conclusions

We second the finding of Zihlman et al. (2004) that Taï, Gombe, and Bossou chimpanzee erupt teeth later than captive samples, although more moderately than suggested by previous analysis. Specifically, we estimate that these wild chimpanzees deviate from captive means by an average -1.3 Z across teeth, rather than the -2.3 Z implied by previous study. With stricter aging requirements,

the effect reduces to -1.1 Z. Contributing to disparities are correction of a field identification error, methods (how age is counted when birth month is unknown, the treatment of cross-sectional data), and addition of new cases. The high end of the captive range was also underestimated in Zihlman et al. (2004).

Samples are still small enough, and methodology enough at issue, that we are still at the stage of describing our samples, rather than demonstrating statistically that wild and captive samples are drawn from different populations. Still, the findings gain strength in that a series of studies (catarrhines and a generalized mammals) find later tooth emergence in wild or poor environments to some degree.

The natural deaths studied here effectively sum or conflate effects of being wild with effects of early death. Evidence that early death is an important contributor to delay in tooth emergence includes: the younger deaths (<9 years of age) were more delayed than the older and were more often accompanied by disease or debilitation, and that juvenile deaths have higher occurrence and severity of dental anomalies than adult deaths. Lastly, our best estimate of a wild effect not confounded by death, from live-capture of olive baboons, finds an effect half the magnitude (ca. -0.5 Z), and of a reverse pattern compared to these chimpanzees. Thus, present findings for these wild natural deaths of chimpanzees are not likely applicable to all wild primates in the past or present.

Emergence of the first permanent molar, especially used to calibrate growth rates in the fossil record, is insufficiently constrained by present data. The sole case that gives information on first permanent molars is Piment (11788), who died at 3.76 years of age. Her M¹ had not yet erupted, which suggests a Z-score ≤ -1 . If we compare her mandible, however, M₁ was more than likely erupted (a delay of ≥ -1 Z). Until more information becomes available, M₁ emerging ca. 1 SD late, around $3\frac{2}{3}$ – $3\frac{3}{4}$ years of age, is conservative, while still inline with the case in hand. Living wild chimpanzees may well be characterized by a lesser delay; only study of living wild subjects or existing museum collections of wild-shot individuals can provide the answer.

Poor environments are known to delay tooth eruption, and, as shown by experimental data, may leave timing of tooth formation less affected. This may be because tooth emergence is hindered by diminished facial growth, which crowds teeth, or because of other pervasive factors. But just as there is no single poor environment, there is no single wild environment. Extreme or longstanding debility is expected to leave signs in teeth and bone; these signatures are important when evaluating individual deaths. For evaluating fossils of individuals who died as children, taphonomy may be critical, and predator accumulations may be fundamentally different from intentional burials in health and disease background.

Uncertainties remain: a group of six-year-olds with late I¹, but imprecise ages, may attest to a major post-weaning impact of poor conditions. If, on the other hand, they are all below or well below 6.5 years of age, the wild effect over the entire dentition is much closer to -1 Z and fairly steady. Precise ages of these cases could be established in the future.

As new techniques reveal the actual age at death of juvenile hominids, we are accumulating data that can establish age of tooth emergence in extinct species. When our samples increase to more than one individual per species, we can begin to analyze these data as cross-sectional records. This means that emergence age should be established as a midpoint of age between those with unerupted and erupted teeth. If, as samples accumulate, we only average ages of subjects with the tooth already emerged, we will overestimate age of tooth emergence.

Further study has only convinced us that these data are more and more interesting, with intriguing complexities. More data can be brought to bear on questions in the future by investigating the

wild-shot collections of the past, continuing collection of natural deaths, and noting teeth erupted whenever living wild chimpanzees are examined.

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Appendix. Supplementary material

Supplementary data related to this article can be found online, at doi:10.1016/j.jhevol.2010.08.006.

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