Dental microstructure records life history events: A histological study of mandrills (*Mandrillus sphinx*) from Gabon

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A B S T R A C T

Accentuated lines in dental microstructure are hypothesized to correlate with potentially stressful life history events, but our understanding of when, how and why such accentuated lines form in relation to stressful events is limited. We examined accentuated line formation and life history events in the teeth of three naturally deceased mandrills (*Mandrillus sphinx*, Cercopithecidae), for whom we had detailed life history information. We determined the ages at formation of accentuated lines in histological tooth sections and used dates of birth and death to calibrate dental histology to calendar time and individual age. We found accentuated lines that matched their mother's resumption of sexual cycles in two individuals, and possibly in the third individual. The subjects also formed lines when their mothers were mate-guarded by males or wounded. Accentuated lines matched the birth of the next sibling in one of two cases. Both females formed accentuated lines when they experienced their own sexual swelling cycles, but lines did not match all sexual swelling cycles. Mate-guarding matched an accentuated line in one case, but not in another. Lines matched all three parturitions in the two females. Changes in alpha male and captures did not consistently coincide with accentuated line formation, but repeated captures were associated with lines. Using simulated data, we show that the observed number of matches between lines and events would be very unlikely under a null hypothesis of random line formation. Our results support the hypothesis that some life history events are physiologically stressful enough to cause accentuated line formation in teeth. They contribute to our understanding of how primate life histories are recorded during dental development and enhance our ability to use teeth to reconstruct life history in the absence of direct observation.

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1. Introduction

Life history theory explains the scheduling of key events across the lifetime, such as weaning, menarche, first reproduction, parturition, and death, as a product of natural selection, to maximize reproductive success (Stearns, 1989; Promislow and Harvey, 1990; Charnov and Berrigan, 1993; Janson and van Schaik, 1993). The scheduling of life history events evolves in response to trade-offs between energy devoted to growth and energy devoted to reproduction (Stearns, 1992; Charnov, 2001) and between parental investment in current vs. future offspring (Trivers, 1972) and is

highly dependent on age-specific mortality rates (Promislow and Harvey, 1990; Charnov, 2001). In comparison to other mammals, primates grow and develop more slowly; they begin reproducing late and have long gestation periods, juvenile periods, interbirth intervals, and lifespans (Stearns, 1983; Harvey and Clutton-Brock, 1985; Charnov and Berrigan, 1993; Ross, 1998). In primates, diverse life history strategies have evolved in response to different mortality risks, body sizes and environments, and changes in life history strategies mark important points in primate evolution (Harvey and Clutton-Brock, 1985; Dirks and Bowman, 2007). Although understanding the scheduling of life history events is key to the study of primate evolution, data on the timing of these events are not always easily collected. For example, we cannot obtain direct life history data for extinct primates, and primates living in dense rainforests cannot be studied easily. We therefore need

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proxies for the scheduling of life history events. Fortunately, teeth can hold important clues to life history and can be preserved for long periods after death and under extreme conditions (Hillson, 1996, 2014; Irish and Scott, 2015; Guatelli-Steinberg, 2016; Smith, 2018). Herein, we test the hypothesis that specific life history events are recorded in dental microstructure.

1.1. How dental enamel forms

Dental enamel is the hardest tissue in the body (Boyde, 1989; Park et al., 2008; Simmer et al., 2010; Beniash et al., 2019). It is formed through a process of amelogenesis, consisting of pre-secretory, secretory, and mineralization phases (Boyde, 1965; Robinson et al., 1981; Robinson, 2007; Humphrey et al., 2008a). After ameloblasts differentiate during amelogenesis, they begin secreting enamel matrix from their distal surface. As matrix secretion increases, a cellular extension forms known as the Tomes' process (Warshawsky and Vugman, 1977; Humphrey et al., 2008a). The Tomes' process extending from fully functioning ameloblasts has different secretory regions for prismatic and interprismatic enamel. Prismatic enamel is secreted through the distal surface of the Tomes' process as a proteinaceous matrix impregnated with hydroxyapatite crystallites with their long axes perpendicular to the secretory surface. At the proximal portion of the Tomes' process, a second secretory surface secretes matrix in which the crystallites are aligned perpendicular to the distal surface of the ameloblast, creating the interprismatic enamel. Prismatic and interprismatic enamel therefore have crystallites oriented in different directions. The forming fronts of the two types of enamel are offset by the length of the Tomes' process and the interprismatic enamel forms a pit into which the prismatic enamel is secreted. The boundary of the prism itself is enclosed by a protein sheath (Boyde, 1964; Moss-Salentijn et al., 1997; Diekwisch et al., 2002; Kierdorf et al., 2014; O'Meara et al., 2018).

Ameloblast activity is regulated by circadian clock genes (Lacruz et al., 2012) and enamel has incremental growth lines reflecting this rhythm, as well as subdaily and longer period biorhythms. This means that teeth preserve a record of their own incremental growth through daily increments which reflect a 24-h cycle of matrix secretion and deposition. Regular, longer-period growth lines (also known as Retzius lines) are separated by a number of these daily lines (the periodicity), which is fixed for an individual in primates (reviewed in Dean, 2000a, b; Simmer and Hu, 2001; Smith, 2008; Antoine et al., 2009; Simmer et al., 2010; Antoine et al., 2019). In normal, healthy primate enamel the rhythmic longer period line pattern is thought to be caused by a periodic constriction in prism diameter in which the interprismatic matrix expands at the expense of prisms themselves (Risnes, 1990, 1998). Since the diameter of the prism reflects that of the prism-forming portion of the Tomes' process, the longer period lines may be a rhythmic constriction near at the distal secretory face of the Tomes' process (Risnes, 1990, 1998).

Disruptions of the normal secretory ameloblast activity during tooth formation also leave traces in the enamel (Wilson and Shroff, 1970; Rose, 1977; Hillson, 1996; Schwartz et al., 2006; Witzel et al., 2008; Antoine et al., 2019). These disruptions are visible in optical microscopy as accentuated lines running parallel to the longer period lines (Amprino and Camanni, 1956; Weber and Eisenmann, 1971; Rose, 1979; Norén, 1984; Goodman and Rose, 1990; Hillson, 1996). They are pronounced, irregularly spaced, and can, but do not always, coincide with the longer period lines (contra Hillson, 2014). Accentuated lines appear in all teeth that form simultaneously, indicating their chronologic nature (Sarnat and Schour, 1941; Goodman et al., 1984). They are thought to relate to metabolic disturbance and are therefore often referred to as 'stress lines'.

Such metabolic disturbances can be changes in blood pH, which can affect the process of mineralization, changes in body temperature, which can disrupt cellular activity if too high (Dean and Elamin, 2014), and disturbances in calcium metabolism, causing changes in ameloblast metabolism and movement (Rose, 1979).

Scanning electron microscopic analyses of enamel show that accentuated lines are broad, hypomineralized bands with varying types of abnormal structure and zones of aprismatic enamel (Rose, 1979; Kierdorf and Kierdorf, 1997; Kierdorf et al., 2000, 2021; Witzel et al., 2008). They appear to occur when ameloblast secretory activity is disrupted and reduced to the extent that the Tomes' process regresses and in some cases, is completely lost. In some ameloblasts along the forming front, secretion is not completely disrupted, but occurs at the proximal secretory surface, creating a band of aprismatic enamel (Kierdorf and Kierdorf, 1997; Kierdorf et al., 2000, 2021; Witzel et al., 2008). The fact that these bands of aprismatic enamel are also hypomineralized (Rose, 1979) suggests that the matrix has a lower mineral content than it would normally have. The final mineral content of enamel is created by adding to the length and thickness of existing crystallites during the maturation phase; the initial number of crystallites secreted in the matrix does not increase (Fincham et al., 2000; Simmer et al., 2010). Because accentuated lines are formed during the secretory stage and remain when maturation is complete, they may contain fewer crystallites when they initially form than normal enamel does.

An alternative explanation for the appearance of accentuated lines is that substitution of elemental ions at calcium sites in the hydroxyapatite lattice may disrupt the crystalline structure of enamel at these sites (Boanini et al., 2010). A study of trace element signatures in primate dentine showed increases in elemental ions (strontium, barium and lead) that substitute for calcium (Ca^{2+}) in the apatite at accentuated lines (Austin et al., 2016) and a similar pattern has been shown for barium in enamel (Austin et al., 2013; Smith et al., 2018). Ameloblast calcium transport depends on the amount of extracellular calcium (Sasaki and Garant, 1987) and cortisol secreted during activation of the hypothalamic pituitary adrenal axis (HPA axis) may disrupt calcium absorption and the balance between potassium and sodium within the ameloblast (Temple, 2019), creating an even less crystalline structure than normally found within the impure biological apatite. A recent study of the mineral content of accentuated lines showed a lower phosphate content than in the surrounding enamel, which would also disrupt the apatite structure (Vacková et al., 2021).

After a time, depending on the duration of the stress, some of the secretory ameloblasts re-establish their normal morphology, with the formation of new Tomes' processes and resumption of the deposition of prismatic enamel (Witzel et al., 2008). The hypomineralized accentuated lines are not repaired during later stages of amelogenesis, however, and so persist in the enamel (Witzel et al., 2008). The severity of the impairment resulting in the microstructural abnormalities in enamel is hypothesized to depend on both the intensity and duration of a stress event, as well as being related to the age of the secretory ameloblast and its corresponding location (Witzel et al., 2008; Kierdorf et al., 2021). Older ameloblasts closer to the future enamel surface, those that differentiated earliest along the forming front, have less ability to rebound and continue normal secretion than younger ameloblasts closer to the enamel dentine junction. In some cases, ameloblasts close to the end of their secretory phase are unable to resume functioning at all and enamel secretion ceases, leaving hypoplastic defects on the surface of the teeth, while younger ameloblasts along the same forming front continue secretion (Witzel et al., 2008; Kierdorf et al., 2021).

1.2. Accentuated lines and physiological 'stress'

The link between accentuated lines and physiology underpins the hypothesis that accentuated lines record periods of stress (Boyde, 1989; Goodman and Rose, 1990; Dirks et al., 2002, 2010; FitzGerald and Saunders, 2005). Evidence that accentuated lines record stress comes from a relationship between captures, anesthesia, enclosure transfers and hospitalization and the formation of accentuated lines in rhesus macaques (*Macaca mulatta*) and a juvenile gorilla (*Gorilla gorilla gorilla*; Bowman, 1991; Schwartz et al., 2006; Austin et al., 2016). Furthermore, research on the same rhesus macaques and on juvenile wild chimpanzees (*Pan troglodytes verus*) suggests connections between the formation of accentuated lines and illness, periods of dehydration or diarrhea and major disruptions in body mass trajectory (Bowman, 1991; Smith and Boesch, 2015; Austin et al., 2016). Finally, recent work on pigs (*Sus scrofa*) showed a correlation between surgical processing, abrupt separation from the mother, and vaccination of piglets and the formation of accentuated lines in teeth (Skinner and Byra, 2019).

Many life history events include disruptions to the individual's social environment, such as rejection by its mother during weaning, the onset of reproductive behaviors, changes in social status and novel relationships. In such situations, the HPA axis is activated, and hormones such as glucocorticoids are released into the bloodstream, enabling the individual to cope (Sapolsky, 1987, 2000). Due to this physiological disruption and hormonal response, important life history events in primates may also correlate with the formation of accentuated lines (Dirks et al., 2002, 2010). This relationship is well established for one life history event: the neonatal line forms in teeth at birth (Schour, 1936; Norén, 1984; Eli et al., 1989; Zanolli et al., 2011; Witzel, 2014; Kurek et al., 2016).

Several studies suggest that physiological or psychological stress related to other life history events and phases, such as weaning, sibling birth, sexual cycles and parturition in female primates, is similarly associated with the formation of accentuated lines in teeth. The teeth of two female, wild hybrid baboons (*Papio anubis* x *Papio hamadryas*) showed accentuated lines when they were just over 12 months old, leading to the hypothesis that these lines represent physiological stress associated with the acquisition of nutritional, locomotory and psychological independence from the mother, peaking when the mother resumes her menstrual cycle and consorts with the much larger males (Dirks et al., 2002). Accentuated lines in two anubis baboons (*P. anubis*) also coincided with the age at which this species undergoes dietary transitions during weaning (Dirks et al., 2010). Perhaps most intriguingly, the hybrid baboons showed a distinct cyclical pattern of accentuated lines beginning at about the age of 4 years, when female baboons undergo menarche (Dirks et al., 2002). Studies of various species of mammal have identified markers in teeth which may correspond to parturition (Okada, 1943; Klevezal and Myrick, 1984; Trunova et al., 1999). Despite this suggestive evidence, however, no life history data were available for the individual animals in any of these studies to confirm the hypothesized links between accentuated lines and life history events. A study of rhesus macaques with known life histories found trace elemental banding in dentine occurred in two subjects when their mothers conceived subsequent offspring, when one subject conceived herself and at the time of a spontaneous abortion and the authors attributed this to stress physiology (Austin et al., 2016). The precise ages for the elemental banding were determined histologically. A recent study of human dental cementum found evidence that parturition and menopause are recorded in teeth, but although records of these events were available for the subjects, the timing of the cementum layers was reconstructed rather than determined precisely (Cerrito et al., 2020). A further study using the same technique on cementum from rhesus macaques with known life histories found that weaning, parturitions, trauma, and illness were all recorded with an error range of 0.43 years (Cerrito et al., 2021).

1.3. This study

To test whether specific life history events cause physiological stress that is associated with accentuated lines, we need a study of accentuated line formation in individuals for which full life history data and the chronology of dental development are both available (Dirks et al., 2002). Here, we combine longitudinal observational data with dental histology of three naturally deceased mandrills (*Mandrillus sphinx*, Cercopithecidae). Mandrills are large, semiterrestrial, forest-dwelling and social primates. They exhibit the greatest sexual dimorphism of any living primate with males having 3.4 times the body mass of females (Setchell et al., 2001). They are endemic to Gabon, Republic of Congo, Equatorial Guinea and Cameroon (Grubb, 1973). Their dense rainforest habitat makes close observation of their social interactions and life history in the wild challenging (Rogers et al., 1996), but the Centre Internationale de Recherches Médicales, Franceville (CIRMF), Gabon, houses a large, semifree-ranging colony of mandrills on which most of our knowledge of mandrill growth, development, social systems, reproductive behavior and life history is based (e.g. Setchell et al., 2001, 2005a, b; Setchell and Wickings, 2004a, b; Setchell, 2016). CIRMF mandrills live in multimale, multifemale groups, with a polygynandrous mating system and a strong male hierarchy in which males attain alpha rank via physical aggression or succession (Setchell et al., 2005b; Setchell, 2016). Female ranks are stable and inherited from their mother (Setchell et al., 2008).

We aimed to: 1) determine the ages at formation of accentuated lines in the teeth of three mandrills, and 2) test the hypothesis that accentuated lines in histological tooth sections are associated with the physiological stress related to specific life history events, including the mother's resumption of cycling, the birth of siblings, and menarche and parturition in females (Table 1). If this hypothesis is supported, we predict that these events will match the formation of accentuated lines in the mandrills' teeth. In addition to life history events, social interactions can also be a source of stress and may therefore be visible on a histological level. Although the focus of this study lies in the association between accentuated line formation and life history events, we also test whether accentuated line formation is associated with changes in alpha male, which is accompanied by changes in the social environment that may be stressful (Stavisky et al., 2001; Barrett et al., 2002; Muller and Wrangham, 2004; Sapolsky, 2005; Crockford et al., 2008; Setchell et al., 2010), and veterinary captures, which are known to cause physiological stress and relate to accentuated line formation in other primates (Bowman, 1991; Schwartz et al., 2006; Austin et al., 2016). Finally, there are many accentuated lines in a tooth and some of these lines will match life history events by chance. To test whether the number of matches we identified exceeds what would be expected by chance, we simulated data for the ages at which lines formed in the teeth for each individual and compared the number of matches in these simulations with our observations.

2. Materials and methods

The mandrill colony at CIRMF was founded in 1983−1984, when eight females (aged 2−6 years) and seven males (aged 2−4 years) were released into a 6-ha naturally rain-forested enclosure and left to breed naturally (Feistner et al., 1992). In 1994, two matrilines and several males were moved into a second enclosure of 3.5 ha to establish a second semifree-ranging group. From the foundation of

Table 1
Summary of hypothesized stressful events and associated predictions.

Type of event	Hypothesized factor causing physiological stress that disrupts the formation of dental tissues in the offspring	Timing of accentuated lines
Life history	Decreased attention, maternal rejection and attention of large males when the mother resumes reproductive cycling	When mother resumes cycling
		When mother is mate-guarded
	Decreased attention and maternal rejection when siblings are born	When a sibling is born
	Increased male attention and physiological changes during first and subsequent reproductive cycles	When a female reaches menarche and has subsequent cycles
		When a female is mate-guarded
	Psychological and physical changes during first and subsequent parturitions	At parturition
Social environment	Instability in the group when alpha male changes	When the alpha male changes
Capture	Veterinary captures	When an individual is captured

the colony in 1983 until 2006, when data collection for this study ended, 307 animals were born into the colony, of which some were removed, escaped or died (Setchell, 2016). Group size per enclosure ranged from the original 15 to a maximum of 104, a size comparable to smaller groups of mandrills observed in the wild (Rogers et al., 1996). The CIRMF enclosures are wire-fenced and contain pens to provide food twice a day which are also used to capture the animals periodically.

Females in this population wean infants at a median age of 7.7 months (range 6.1−38.6 months, based on the median interbirth interval minus the median gestation length (Setchell et al., 2002). They experience their first sexual cycle at a median age of 3.6 years (range 3.2−4.6 years; Setchell and Wickings, 2004b) have a median age at first birth of 4.7 years (range 3.3−6.1 years; Setchell et al., 2002) and reach their full adult size at 7 years. Males experience puberty at a similar age to females, but then continue to grow until they are 9−10 years. The mean age at first reproduction for males is 11.6 years, by which time females already have several offspring (Setchell et al., 2005a).

We obtained crania and mandibles of naturally deceased mandrills from the CIRMF colony. Of these remains, we selected two adult females and one adult male for whom life history data were available for the period of their dental development (Table 2).

2.1. Life history data, changes in alpha male and captures

We used near-daily records of the prominent cyclical sexual swellings exhibited by female mandrills (Setchell and Wickings, 2004a) to establish the female reproductive cycle for the two females and the mothers of all three subjects (Table 3). Studies of baboons (Wildt et al., 1977; Shaikh et al., 1982) and zoo-housed mandrills (Phillips and Wheaton, 2008) show that enlarged sexual swellings correlate with increased estrogen levels during the follicular phase, and that ovulation occurs during the last few days of maximal swelling. We used these data on the mother's

reproductive cycle to determine the ages of the subjects when their mothers resumed their sexual cycling after parturition.

We collated dates on which the mothers and the females themselves were mate-guarded from daily records of the colony. Mate-guarding is an unambiguous behavior whereby a male closely and persistently follows a female, interacts with her sexually, and attempts to prevent other males from gaining access to her (Setchell et al., 2005b).

We obtained the dates of births of the subjects' younger siblings and dates on which the two females themselves gave birth from colony records. Dates are accurate to the day for all births that took place before 2006 (end of data collection by Setchell), after which dates of birth are accurate to the week, based on the first observation of the new infant by CIRMF staff, the known gestation period of mandrills (175 days; Setchell et al., 2002) and female cycling data.

We collated the dates at which the alpha male changed from colony records. Changes in alpha male involve an obvious change in the direction of submissive behavior between males from one day to the next (Setchell et al., 2006). In some cases, we know the exact date of the change from daily observations, while in other case we know the approximate timing because colony observations were less regular.

Finally, we collated dates of veterinary captures. These captures occur at least once per year for annual check-ups. Captures involve closing animals in the feeding pen and delivering intramuscular injections of Imalgene1000 using a Telinject blowpipe (10 mg/kg of body mass; Rhone-Mérieux, Lyon, France; Wickings and Dixson, 1992). Once anesthetized, animals are transported to the primate center for veterinary examination. Afterwards, the animals are placed in the covered feeding pen to recover, and released into the enclosure when fully awake, usually on the day of capture. Occasionally the veterinarians keep the animals in cages at the primate center for treatment or protocols and sedate them multiple times over a short period. This happened to one study subject (5D3A).

Table 2
Information on the study subjects and teeth sampled. Female rank is expressed as both absolute rank and as the percentage of females dominated to account for demographic changes over time (Setchell et al., 2002). Dates of birth and death are accurate to the day, apart from 17E2 whose death we estimated from the state of decomposition.

ID	5D3A	PB	17E2
Sex	Female	Female	Male
Date of birth	23/02/2001	26/04/2002	17/02/2002
Date of death	09/09/2011	09/09/2011	24/06/2010
Age at death (years)	10.6	9.4	8.4
Mother's ID	5D3	P	17E
Mother's rank at birth	8 of 21 (68%)	28 of 28 (0%)	13 of 13 (0%)
Own rank from age 3.5 years	11 of 30 (66%)	36 of 36 (0%)	Variable throughout life
Reason for death	Accident	Accident	Unknown (found in state of decomposition in the enclosure)
Teeth sampled	RI_1, RI_2, RC_1, LP_3, RP_4, LM_1, LM_2, LM_3	LI_1, LI_2, LC_1, LP_3, LP_4, RM^1, RM^2, RM^3	RI_1, RI_2, LC^1, LP^3, LM_1 LM^2, LM^3
Teeth with incomplete roots	—	RM^3	LC^1

L = left, R = right.

Table 3
Scoring system for sexual swellings in female mandrills (after Setchell 1999).

Score	Description
0	Flat, no swelling. Sexual skin is pale
+1	Small swelling, increasing in size but not maximal. Sexual skin is pinkish
+2	Medium swelling, increasing in size, but not maximal. Sexual skin is pinkish
+3	Maximum swelling, sexual skin is turgid and bright pink/reddish
BD	Day of sexual skin breakdown, clear decrease in swelling turgidity and size from previous days
−3	Large, post-breakdown swelling, decrease in swelling and loss of coloration
−2	Medium swelling, decreasing in size
−1	Small swelling, decreasing in size
P	Pregnant, small swelling. Skin is redder and skin is more wrinkled than for +1

2.2. Samples and sectioning

When animals were not recorded as present during daily censuses, CIRMF staff searched the enclosures for dead animals. If they found a dead animal, they collected the remains and placed them in plastic bags for controlled decomposition in a designated area, keeping track of their ID numbers for later reference. Staff made every effort to keep material complete, but some teeth were lost post-mortem. Staff cleaned the remains using salt and alcohol, with minimal use of bleach.

We shipped the material to the UK, where we selected at least one of each tooth type per individual to cover the maximum developmental time: from the initiation of the M1 prebirth until the end of M3 root development. We used mandibular teeth from the same quadrant whenever possible but in some cases we used the antimere (contralateral) or isomere (maxillary) due to damage to the teeth. For PB, we used the M^1 and the protoconid of the M_1. For 5D3A we used only mandibular teeth. For 17E2, we used the C^1 and P^3.

We extracted and cleaned the teeth. For sectioning, we followed a standard histological preparation procedure (Reid et al., 1998). We coated each tooth with cyanoacrylate to prevent chipping and breakage and cut 180−200 μm ground longitudinal sections using a Micro Slice II with a diamond edge blade. For anterior teeth we cut through the midline on the axial plane and for posterior teeth, we cut through the mesial and distal cusp planes to cover maximum tooth formation. We polished sections with a Logitech PM2 lapping machine, lapping them with 3 μm aluminum oxide powder to a final thickness of 91−113 μm. We cleaned the sections ultrasonically, with distilled water, graded alcohol baths and Xylene and used Histomount® as mounting medium.

2.3. Histological analysis

We analyzed the sections using an Olympus BX51 microscope with polarized light and neutral density filters mounted with a Q-Imaging Micropublisher v. 3.3 RTV (Q-Imaging, Surry) and used Improvision Openlab v. 5.0.2 image analysis software (Improvision, Berkeley). We transferred micrographs to Adobe Photoshop CS5 to create high resolution montages, using these to mark accentuated lines.

Methods for scoring accentuated lines are debated (FitzGerald and Saunders, 2005; Witzel et al., 2008), and we scored lines as accentuated whether they were visible for at least 75% of the distance from the enamel dentine junction to the surface of the tooth (Goodman and Rose, 1990; FitzGerald and Saunders, 2005; FitzGerald et al., 2006; Antoine et al., 2009). Although the cause of variation in the appearance of accentuated lines is not yet fully understood, it is thought that the duration and severity of the stressor affect the line appearance (e.g. Rose, 1977; Goodman and Rose, 1990; Witzel et al., 2008), as well as the age and subsequent position of the secretary ameloblast (Witzel et al., 2008). We

therefore only included accentuated lines that stood out strongly in low-resolution imaging (4× objective) of a whole tooth section and remained clearly visible when a section was slightly out-of-focus. These accentuated lines can be distinguished clearly from less strongly defined disturbances in the enamel.

We established the position of each accentuated line using counts of the daily increments (cross-striations), following established methods in primate dental development (for detailed methods see Dean, 2000a; FitzGerald and Saunders, 2005; Smith, 2008; Hillson, 2014), and calculated the periodicity for each animal (the number of daily increments between adjacent longer period lines). We repeated sets of measurements to control for intra-observer error. Since accentuated lines mark brief periods of disruption, they are recorded in all teeth developing at the same time. Therefore, each accentuated line provides a temporal anchor point to match teeth developing simultaneously (Dean et al., 1993; Reid et al., 1998; Dirks et al., 2002; Schwartz et al., 2006; Hupková et al., 2015). We matched all accentuated lines in each tooth with the overlapping sections of the other teeth of that individual, yielding a continuous record of accentuated lines from the first increments of the M1 to the last increment formed, which coincided with end of dental development (5D3A) or with death (17E2, PB; Fig. 1). We focused on accentuated lines in enamel but used lines in dentine to improve confidence in measurements and when enamel formation had ended. SAML performed all dental histology, with guidance from WD.

2.4. Matching accentuated lines to life history events

We first report the number of accentuated lines we found in the teeth of each mandrill. Then, to test our predictions, we examined whether life history and stressful events matched the formation of these lines. Teeth have a daily rate of tissue deposition, hence, in theory we should be able to detect an exact match between a stressful event and the effect on dental tissue deposition. However, daily precision is unrealistic when measuring and matching multiple teeth (Antoine et al., 2009). One effect of ameloblast disruption on enamel formation toward the surface of a tooth is a narrowing and bending of Retzius lines, creating more narrowly spaced perikymata (Witzel et al., 2008; Temple, 2014). This narrowing may account for the appearance of accentuated lines as coincident with Retzius lines (FitzGerald and Saunders, 2005; Hillson, 2014). To control for this, we considered an accentuated line to match an event if it occurred from 3 days before to 3 days after the day of an event (inclusive). This 7-day range is equal to the mean periodicity in mandrills (range 6−8 days; Lemmers, 2017; Dirks et al., 2020) and none of our subjects had periodicities greater than 7. A previous study of accentuated line formation reported errors of 1−9 days across teeth when ages of matching lines were calculated independently in each tooth (Dirks et al., 2010). A 7-day matching window is therefore a stricter criterion than the maximum error of 9 days
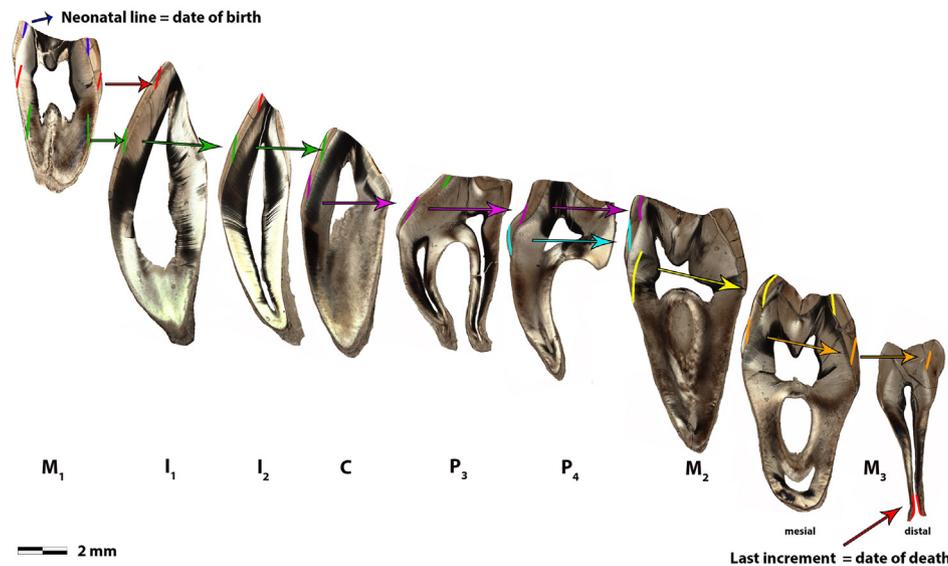
Figure 1. Schematic overview of the procedure used to match accentuated lines across teeth in a dentition. The neonatal line in the first molar (top left, blue line, marked with blue arrow) links the whole sequence to calendar time based on the date of birth. Colored lines in teeth and arrows between teeth represent examples of how an accentuated line associated with a specific point in time is present in all teeth forming at that time. The third molar was still developing at death, so the sequence can be linked to the known age at death using the last increment formed (bottom right). Micrographs made with 4× objective. Only some accentuated lines are visible at this magnification. We conducted the matching procedure at 20× and 40× magnification to include all the lines. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

and ensures that we do not overinterpret any possible matches between accentuated lines and stressful events. If an accentuated line did not fall within ±3 days of an event, we did not consider it a match. We also report the effect of increasing the matching window to 9 days and report the number of days to the closest accentuated lines, so that the reader can assess the matches for themselves. We report the dates and ages for all accentuated lines in the Supplementary Online Material (SOM).

2.5. Comparing observed matches to chance expectations

Given that there are many accentuated lines in a tooth, some of these lines will match life history events by chance. To compare the number of matches that we found to the number expected by chance, we simulated line formation ages (in days) and checked for matches with the observed life history events. For each individual, we drew a number of simulated lines equal to the number of lines recorded in the study from a uniform distribution across the period covered by each individual's dental records (from first record/birth to last record/death). We then checked for matches with the known events, defining matches in the same way as we did for the observations (i.e., the number of lines that fall within −3 to +3 days inclusive of an event). Where an event lasted for multiple days (e.g., an inflating sexual swelling), we treated the match window as from 3 days prior to the first day to 3 days after the final day, again inclusive. We ran 1000 simulations, plotted the distribution of expected matches and compared it with the observed number for each individual. We also report the proportion of simulated data points that are at least as great as the number of observed counts. This proportion is the probability of the observed level of matching occurring by chance, and is equivalent to a one-tailed *p*-value, which we also report, but we did not define an arbitrary a priori alpha level. As with the observed data, we also repeated the simulations for a 9-day match window (−4 to +4 days inclusive of an event). We ran simulations in R v. 4.0.4 (R Core Team, 2021) and provide the annotated code and csv data files in the SOM.

3. Results

3.1. Mandrill PB

The cusps of female PB's M_1 were worn down past the neonatal line, but the root of her third molar was open, allowing us to calibrate her accentuated line sequence to her known age of death. PB's dentition covered the period from age 3 weeks until her death at age 9.38 years. This is 99% of her life span, during which 32 accentuated lines formed in her teeth (Fig. 2; SOM Table S1).

PB formed 4 accentuated lines in the first 0.50 year of her life, then no more until she was age 1.12 years. She was captured at age 0.19 years and there was a change in alpha male in her group when she was aged 0.71 years, but no accentuated lines in her teeth matched these events (Table 4). PB's mother, P, resumed her sexual cycle when PB was aged 1.06 years, showing a small sexual swelling for 2 weeks, followed by a short interval with no swelling, then a swelling which increased to maximum, then deflated when PB was aged 1.23 years. No accentuated lines formed in PB's teeth for 30 weeks before P resumed cycling, but two accentuated lines matched P's sexual swelling, the first forming as her swelling increased in size (PB aged 1.12 years) and the second when P had a maximum swelling and was mate-guarded (PB aged 1.22 years; Table 4). P conceived during this swelling cycle and PB formed four accentuated lines during her mother's pregnancy (PB aged 1.22−1.69 years; Table 4). None of these lines matched an alpha male change that occurred when PB was aged 1.42 years (Table 4).

PB's first younger sibling, mandrill PC, was born when PB was aged 1.69 years, with no matching accentuated line in PB's dentition (Table 4). PB formed her next accentuated line at age 2.26 years, matching a change in alpha male (Table 4), and another accentuated line matched a capture at age 2.48 years (Table 4). However, no accentuated lines matched another alpha male change and two other captures during this time, when she was aged 2.40−2.92 years (Table 4).

PB began her first sexual swelling at 3.44 years. One extremely clear accentuated line matched her inflating sexual swelling, and
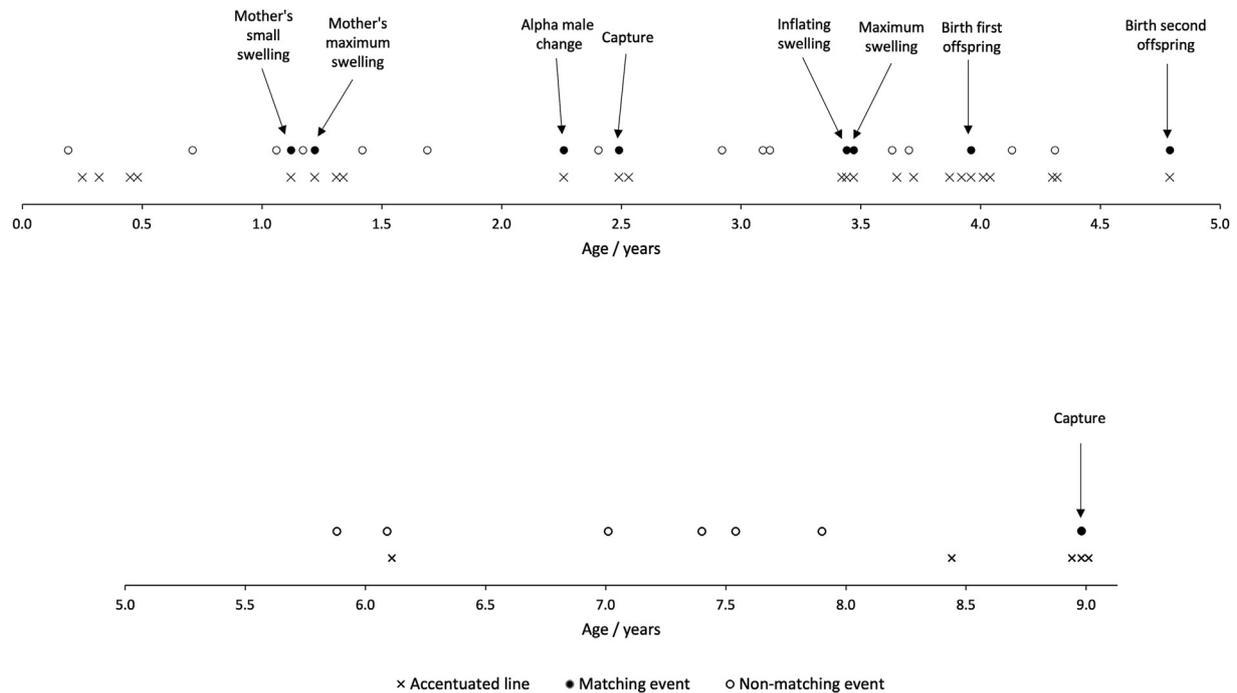
Figure 2. Accentuated lines in the dentition of mandrill PB. Matching events occurred within 3 days of a line and are labeled. Non-matching events are not labeled. The x-axis ends at death and is split at 5 years for convenience.

another extremely clear line matched her maximum swelling (Table 4; Fig. 3). PB conceived during this cycle and formed five accentuated lines during her pregnancy (age 3.46–3.96 years; SOM Table S1). PB's second younger sibling (PD) was born when PB was aged 3.63 years. No accentuated lines matched the estimated date of birth, but one formed 6 days later (Table 4; Fig. 2). PB was caught once while she was pregnant, at age 3.70 years, but none of her accentuated lines matched this capture (Table 4).

PB's first infant (PB1) was born when PB was aged 3.96 years. An accentuated line matched this birth (Table 4), and two further accentuated lines formed during the next 0.17 years, when PB was aged 3.96–4.13 years (Fig. 2). Infant PB1 broke its leg when it was 9 weeks old (when PB was aged 4.13 years), was captured with PB, and euthanized by the CIRMF staff. No accentuated line in PB's dentition matched this event (Table 4).

Based on the date her second offspring (PB2) was born and the gestation period in mandrills, we inferred that PB experienced a sexual swelling cycle when she was aged 4.31 years, when we had no sexual swelling records (Table 4). PB formed an accentuated line 5 days before the estimated date of conception, when we infer that she showed a sexual swelling (Table 4). PB formed no accentuated lines while she was pregnant but did form an accentuated line which matched the birth of PB2, when she was aged 4.79 years (Table 4).

Eight accentuated lines formed between PB2's birth and PB's death at age 9.38 years, but only one of these matched one of the seven captures that took place during this period (Table 4). We have no sexual swelling records for this period. Using a 9-day (±4 days) window rather than a 7-day window did not change the results for PB (data not shown).

Overall, we observed 10 matches for PB using a 7-day match window. This exceeded the maximum number of matches observed by chance in the simulation (9; Fig. 4), corresponding to a one-tailed *p*-value of <0.001. When repeating the simulation using a 9-day window, we obtained 10 or more matches only 1/1000 times (*p* = 0.001; SOM Fig. S1).

3.2. Mandrill 5D3A

We calibrated female 5D3A's dental development to her date of birth using the neonatal line. Her dentition covered from 3 weeks before birth to age 8.55 years. This is 81% of her life span, during which 45 accentuated lines formed in her teeth (Fig. 5; SOM Table S2). We could not assess her dental histology when she was aged 7.02–7.35 years, due to the poor quality of sections.

After the neonatal line, the first accentuated line formed in 5D3A's teeth when she was age 0.16 years, matching a capture (Table 5). After that, no accentuated lines formed for 0.50 years, until 5D3A was aged 0.69 years, although a capture and two alpha male changes occurred during this period (Table 5).

We have no sexual swelling records for 5D3A's mother, 5D3, when 5D3A was aged 0.50–0.63 years. 5D3's sexual swelling was deflating when records resume, suggesting she had just had a sexual swelling cycle, when 5D3A was 0.65 years. No lines in 5D3A's teeth matched this inferred sexual swelling (Table 5). 5D3A then experienced another sexual swelling for which we have partial records. A line in 5D3A's teeth at 0.69 years matched her mother's inflating swelling (Table 5).

5D3A then formed no accentuated lines for 0.73 years, until her mother experienced her next sexual swelling when 5D3A was aged 1.42 years. 5D3 experienced a long maximum swelling, during which she was mate-guarded twice. An accentuated line in 5D3A's teeth matched the second time her mother was mate-guarded (Table 5).

During the following 0.50 years, 5D3A formed one accentuated line at age 1.69 years, while her mother was pregnant. An alpha male change occurred when she was aged 1.88 years, but no accentuated line matched this event (Table 5).

5D3A's next accentuated line matched the birth of her first sibling (5D3B) when 5D3A was aged 1.89 years (Table 5). Following the birth of her sibling, 5D3A experienced a capture (age 2.26 years), another alpha male change (age 2.59 years), and another capture (age 3.1 years). Her mother then had a sexual

Table 4
Dates and ages at which events occurred in the life of mandrill PB, with the date of the closest accentuated line that formed in her dentition and whether we considered it a match. Bold indicates lines with a match (i.e., the line formed within ±3 days of the event).

Date	Age (years)	Own life event	Mother's life event	Date closest accentuated line	Days between event and accentuated line	Considered a match?
26 Apr 2002	0.00	birth		Teeth worn		
05 Jul 2002	0.19	capture		30 Jul 2002	25	N
10 Jan 2003	0.71	alpha male change		18 Oct 2002	84	N
19−30 May 2003	1.0−1.09		small swelling, did not reach maximum	10 Jun 2003	9−20	N
10−17 Jun 2003	**1.12 −1.14**		**small swelling, did not reach maximum**	**10 Jun 2003**	**0−7**	**Y**
26 Jun−01 Jul 2003	1.17 −1.18		inflating swelling	10 Jun 2003	16−21	N
04−18 July 2003	**1.19 −1.23**		**maximum swelling**	**17 Jul 2003**	**0−13**	**Y**
15−16 Jul 2003	**1.22**		**mate-guarded**	**17 Jul 2003**	**1−2**	**Y**
26 Sep 2003	1.42	alpha male change		27 Aug 2003	30	N
03 Jan 2004	1.69		Birth of PC (exact date)	27 Aug 2003	129	N
31 Jul 2004	**2.26**	**alpha male change**		**31 Jul 2004**	**0**	**Y**
20 Sep 2004	2.40	alpha male change		21 Oct 2004	31	N
18 Oct 2004	**2.48**	**capture**		**21 Oct 2004**	**3**	**Y**
29 Mar 2005	2.92	capture		07 Nov 2004	142	N
28 May - 06 Jun 2005	3.09 −3.11		inflating swelling	26 Sep 2005	**112−121**	N
07−21 Jun 2005	3.12 −3.15		maximum swelling	26 Sep 2005	**97−111**	N
03−09 October 2005	**3.44 −3.46**	**inflating sexual swelling**		**04 Oct 2005**	**0−5**	**Y**
10−19 October 2005	**3.46 −3.48**	**maximum sexual swelling?**[a]		**14 Oct 2005**	**0−5**	**Y**
13 Dec 2005	3.63		birth of PD (estimate)[b]	19 Dec 2005	**6**	N
05 Jan 2006	3.70	capture		14 Jan 2006	9	N
13 Apr 2006	**3.96**	**birth PB1 (estimate)**[c]		**10 Apr 2006**	**3**	**Y**
14 Jun 2006	4.13	capture, PB1 euthanized		11 May 2006	34	N
19 Aug 2006	4.31	PB2 conceived (estimate)[d]		14 Aug 2006	5	N
10 Feb 2007	**4.79**	**birth PB2 (exact)**		**07 Feb 2007**	**3**	**Y**
13 Mar 2008	5.88	capture		08 Sep 2008	179	N
28 May 2008	6.09	capture		08 Sep 2008	103	N
30 Apr 2009	7.01	capture		08 Sep 2008	234	N
18 Sep 2009	7.40	capture		08 Sep 2008	375	N
09 Nov 2009	7.54	capture		02 Oct 2010	327	N
19 Mar 2010	7.90	capture		02 Oct 2010	197	N
19 Apr 2011	**8.98**	**capture**		**18 Apr 2011**	**1**	**Y**

[a] Swelling records suggest swelling was +2 not maximum, but it was her first swelling, so likely to have been small, and she conceived.
[b] Date of birth estimated from gestation length and appearance when first observed.
[c] Date of birth estimated from gestation length.
[d] No swelling records available—conception date estimated based on gestation length.

swelling cycle and was mate-guarded (age 3.32−3.39 years) and there was a further alpha male change (age 3.43 years). None of these events matched accentuated lines in 5D3A's teeth, although she formed nine accentuated lines during this period (SOM Table S2).

5D3A's first sexual swelling started when she was aged 3.39 years (Table 5). Her swelling inflated to maximum, and she was mate-guarded. An accentuated line matched the end (breakdown) of her sexual swelling (Table 5). Several days after her sexual swelling ended, another alpha male change occurred (when she was 3.58 years), this time matched by a line in 5D3A's teeth (Table 5). She was captured when aged 3.66 years, but no line matched this event.

5D3A showed a pregnancy swelling after her sexual swelling deflated, which continued until at least 2 months of pregnancy. However, she no longer showed a pregnancy swelling after 4 months (age 3.89 years), did not look visibly pregnant and did not give birth, suggesting that she experienced a spontaneous abortion aged 3.73−3.89 years, but we do not know when this occurred. Two accentuated lines formed in her teeth around this time, but in the absence of information about the exact timing of her abortion, we do not know whether these lines match it (Table 5).

5D3A's next sibling (5D3C) was born when she was aged 3.88 years, and she was captured again at age 4.10 years, but no lines in her teeth matched these events (Table 5).

5D3A had her next sexual swelling at age 4.26 years, and an accentuated line matched 4 days of mate-guarding, when her sexual swelling was at maximum and she conceived infant 5D3A1 (Table 5). Three further accentuated lines formed during her pregnancy (aged 4.33−4.80 years; SOM Table S2), and another accentuated line matched the birth of her first infant 5D3A1, when she was aged 4.80 years (Table 5). Her next accentuated line formed more than 2 months later, when she was aged 5.00 years, and did not match any recorded life history or stressful events.

5D3A formed 14 accentuated lines in the 3.75 years from the birth of 5D3A1 until the end of her dental development at age 8.55 years. We have no sexual swelling records for this period, but we know she had a contraceptive implant and had no further offspring. She was captured 13 times during this period, and accentuated lines matched five of these captures (Table 5).

Using a less stringent 9-day (±4 days) matching window rather than a 7-day window adds an additional match to 5D3A's maximum swelling and mate-guarding at age 3.56 years, and an
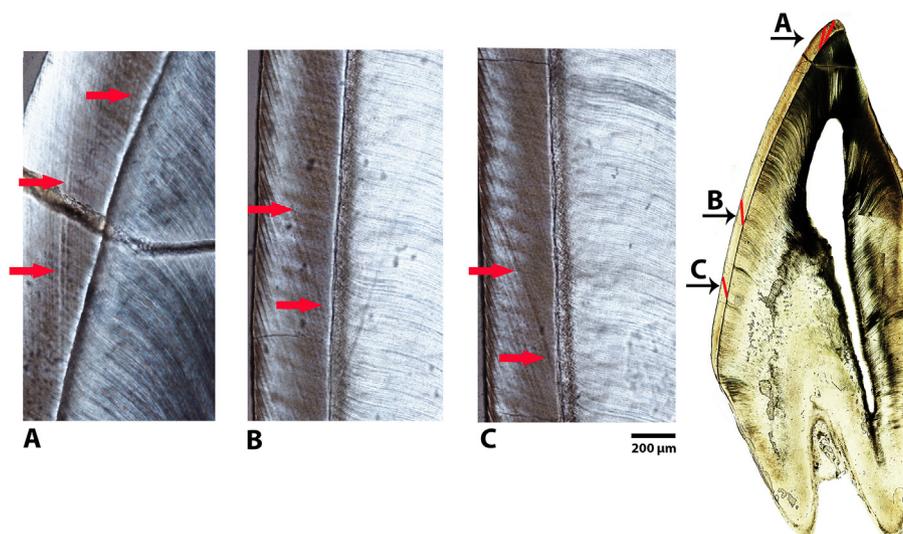
Figure 3. Accentuated lines in PB's canine (left) with their position in the enamel (right). A: Accentuated lines forming at the time when PB's mother resumed her sexual swelling cycle B: Accentuated line forming at the time of PB's first sexual swelling cycle, C: Accentuated line forming at the time of PB's second parturition (birth of PB2). The accentuated lines associated with PB's first sexual swelling were extremely marked, uniform in all teeth forming at the time and were the main connecting point when matching her teeth for dental development.
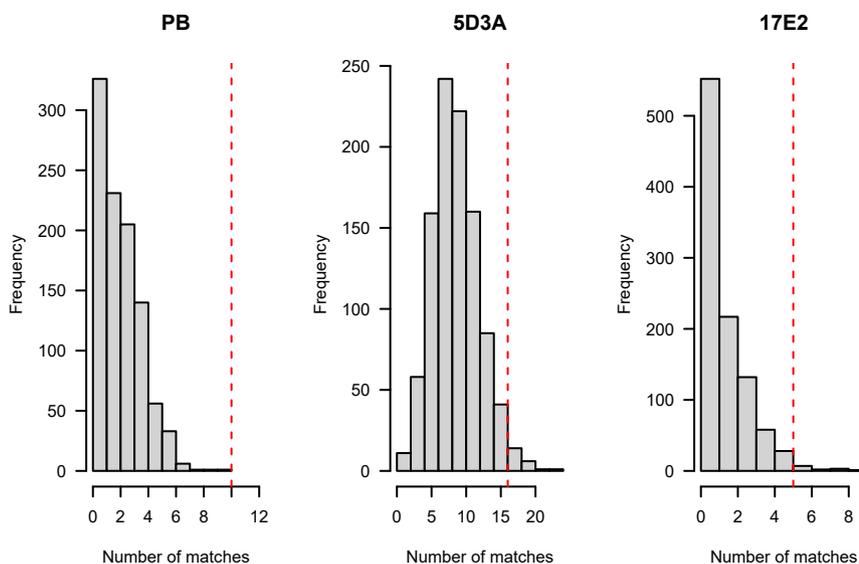

Figure 4. Number of matches between events and accentuated lines in the three mandrills for simulated vs. observed line formation ages. The distributions show the results of 1000 simulations, while the vertical red lines mark the observed number of matches in each animal, when using a 7-day matching window. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

additional three matches to captures (at ages 2.26 years, 3.05 years, 7.67 years; Table 5).

Overall, we observed 16 matches for 5D3A. 16 or more matches were observed 42/1000 times with simulated line ages when using a 7-day matching window ($p = 0.042$; Fig. 4), or 117/1000 times using a 9-day matching window ($p = 0.117$; SOM Fig. S1).

3.3. Mandrill 17E2

Male 17E2's neonatal line was preserved in his M_1 and C^1, allowing calibration to his date of birth. Although 17E2 had an open canine root when he died (aged 8.34 years), the enamel was poorly preserved, and we could not assess the lines in this root. His

accentuated line sequence therefore covers the period from birth until the last increments measurable in his M^3 root at age 6.58 years. This is 79% of his life span, during which 31 accentuated lines formed (Fig. 6; SOM Table S3). However, his dental histology is unreliable from age 4.74 years to the end of his life, and we may have missed accentuated lines that formed during this time.

17E2 formed no accentuated lines in his teeth after his neonatal line until he was aged 0.63 years, although he was caught when he was aged 0.06 years (Table 6). His mother, 17E, resumed her sexual swelling cycle when 17E2 was aged 0.55 years (Table 6). 17E's sexual swelling fluctuated in size instead of increasing to a maximum swelling. She was wounded by a male when 17E2 was aged 0.62 years, matching the first accentuated line in 17E2's teeth
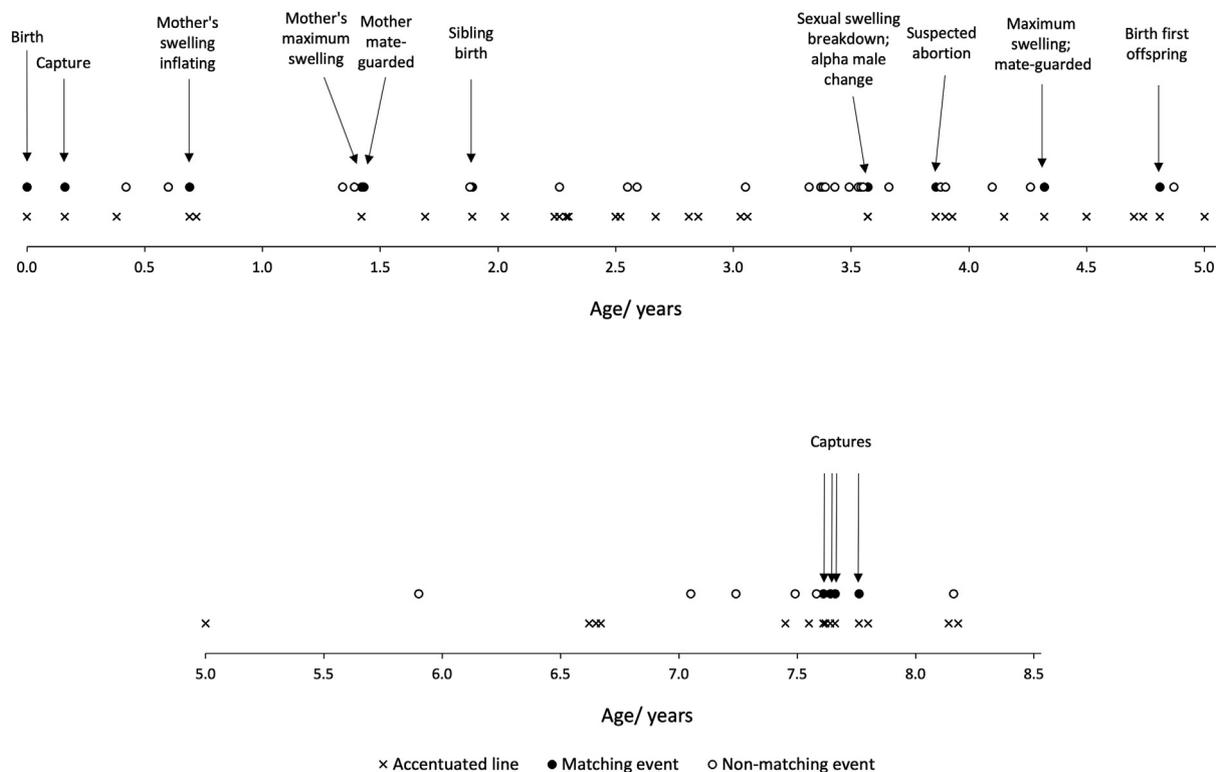
Figure 5. Accentuated lines in the dentition of mandrill 5D3A. Matching events occurred within 3 days of a line and are labeled. Non-matching events are not labeled. The x-axis ends at 8.53 years when dental development ended and is split at 5 years for convenience.

since his birth (Table 6). 17E2 was captured the following week, and another accentuated line matched this capture (Table 6). 17E showed a further sexual swelling when 17E2 was aged 0.70 years but no accentuated line in 17E's teeth matched this. 17E did not conceive during the study period so 17E2 had no younger siblings.

Male 17E2 experienced one change in alpha male in his group but no accentuated line matched that event (Table 6). He was captured seven times at times when we could reliably assess his dental enamel for accentuated lines, but only one of these seven captures matched an accentuated line (Table 6). Using a 9-day (±4 days) matching window rather than 7 days (±3 days) did not change the results for 17E2.

Overall, we observed 5 matches for 17E2. We found five or more matches with simulated line ages 44/1000 times when using a 7-day window ($p = 0.044$; Fig. 4) or 69/1000 times when using a 9-day window ($p = 0.069$; SOM Fig. S1).

4. Discussion

It has long been recognized that changes in life history strategies are important components of primate and human evolution and that aspects of dental development provide a proxy to understand those shifts in the past (e.g., recent reviews in Smith, 2013, 2018; Guatelli-Steinberg, 2016; Dirks, 2018). Our findings support the hypothesized correlation between accentuated line formation and life history events such as the mother's return to sexual cycling and an individual female's own menarche and sexual cycling (Dirks et al., 2002), and parturition (Dean and Elamin, 2014). Our study shows that these events are recorded in enamel and dentine and can therefore be preserved and recognized in an individuals' hard tissue long after the events took place. However, we also found variation in whether the same reoccurring event matches an accentuated line. Like other histological studies of accentuated

lines in the primate dentition (Bowman, 1991; Dirks et al., 2002, 2010; Schwartz et al., 2006; Smith and Boesch, 2015), our study is limited by the small sample size of three animals, due to the time required to analyze each individual. Nevertheless, our detailed survey of line formation over most of these individuals' lifespans supports the hypothesis that some life history events are sufficiently physiologically costly to affect ameloblast function and leave a record of accentuated line formation in teeth. Life history theory emphasizes trade-offs and the fact that events such as menarche, sexual swellings, and parturition can cause enough physiological stress to affect tooth formation demonstrates the hidden costs of reproduction.

4.1. Life history events

Resumption of the mother's sexual swelling cycle is a key event in the weaning process and coincided with the formation of accentuated lines in PB and 17E2. 5D3A also formed an accentuated line during her mother's first recorded sexual swelling cycle following her birth, but her mother may have cycled during the previous few weeks for which we have no sexual swelling observations. These patterns partially support the hypothesis that accentuated lines occur during weaning (Dirks et al., 2010). Weaning conflict is thought to be particularly intense when mothers resume cycling (e.g., Berman et al., 1994; Lee, 1997). The mother's decreased attention to the infant, increased mobility and mating activity when she resumes cycling gives the infant less physical access to her, including decreased time on the nipple and less time carried (Setchell, pers. obs.; Barrett, pers. comm.), which may increase infant stress levels.

Offspring formed accentuated lines on some occasions when their mother was mate-guarded, but not on others. PB formed an accentuated line when her mother was mate-guarded, 5D3A also

Table 5
Dates and ages at which events occurred in the life of mandrill 5D3A, with the date of the closest accentuated line that formed in her dentition and whether we considered it a match. Bold indicates lines with a match (i.e., the line formed within ±3 days of the event).

Date	Age (years)	Own life event	Mother's life event	Date closest accentuated line	Days between event and accentuated line	Considered a match?
23 Feb 2001	**0.00**	**birth**		**23 Feb 2001**	**0**	**Y**
23 Apr 2001	**0.16**	**capture**		**21 Apr 2001**	**2**	**Y**
27 Jul 2001	0.42	alpha male change		12 Jul 2001	15	N
end Sep/start Oct 2001	0.60	alpha male change		01 Nov 2001	30	N
early Oct 2001	0.60−0.63		inferred sexual swelling	01 Nov 2001	20−31	N
30 Oct−06 Nov 2001	**0.68−0.70**		**inflating swelling**	**01 Nov 2001**	**0−4**	**Y**
28 Jun−10 Jul 2002	1.34−1.37		inflating swelling	26 Jul 2002	16−28	N
11 Jul−01 Aug 2002	**1.38−1.43**		**maximum swelling**	**26 Jul 2002**	**0−15**	**Y**
15−17 Jul 2002	1.39		mate-guarded	26 Jul 2002	9−11	N
29−31 Jul 2002	**1.43**		**mate-guarded**	**26 Jul 2002**	**3−5**	**Y**
10 Jan 2003	1.88	alpha male change		15 Jan 2003	5	N
16 Jan 2003	**1.89**		**birth of 5D3B (exact)**	**15 Jan 2003**	**1**	**Y**
29 May 2003	2.26	capture		02 Jun 2003	4	N
11 Sep 2003−08 Jan 2004	2.55−2.87		Irregular cycle	02 Sep 2003	9+	N
28 Sep 2003	2.59	alpha male change		02 Sep 2003	26	N
12 Mar 2004	3.05	capture		16 Mar 2004	4	N
20 Jun−07 Jul 2004	3.32−3.37		inflating swelling	31 Jul 2004	24−41	N
08−17 Jul 2004	3.37−3.39		maximum swelling	31 Jul 2004	14−34	N
08 Jul 2004	3.37		mate-guarded	31 Jul 2004	23	N
10−16 Jul 2004	3.38−3.39		mate-guarded	31 Jul 2004	15−23	N
31 Jul 2004	3.43	alpha male change		21 Sep 2004	52	N
15 Jul−22 Aug 2004	3.39−3.49	inflating swelling		21 Sep 2004	30−68	N
19 Aug 2004	3.49	mate-guarded		21 Sep 2004	33	N
22 Aug 2004	3.49	mate-guarded		21 Sep 2004	30	N
04−08 Sep 2004	3.53−3.54	inflating swelling		21 Sep 2004	13−17	N
09−14 Sep 2004	3.54−3.56	maximum swelling		21 Sep 2004	7−12	N
11−13 Sep 2004	3.55	mate-guarded		21 Sep 2004	8−10	N
14 Sep 2004	3.56	maximum swelling		18 Sep 2004	**4**	N
15 Sep 2004	**3.56**	**sexual swelling breakdown**		**18 Sep 2004**	**3**	**Y**
20 Sep 2004	3.58	**alpha male change**		18 Sep 2004	**2**	**Y**
22 Oct 2004	3.66	capture		24 Sep 2004	28	N
mid-Nov 2004−mid-Jan 2005	3.73−3.89	spontaneous abortion		04 Jan 2004	?[a]	?[a]
09 Jan 2005	3.88		birth of 5D3C (exact)	17 Jan 2005	8	N
31 Mar 2005	4.10	capture		17 Apr 2005	17	N
30 May−09 Jun 2005	4.26−4.29	inflating swelling		19 Jun 2005	10−20	N
13−18 Jun 2005	**4.30−4.31**	**maximum swelling**		**19 Jun 2005**	**0−6**	**Y**
19−22 Jun 2005	**4.32−4.33**	**mate-guarded**		**19 Jun 2005**	**0−3**	**Y**
14 Dec 2005	**4.80**	**birth first offspring (5D3A1)**		**15 Dec 2005**	**1**	**Y**
05 Jan 2006	4.87	capture		23 Feb 2006	49	N
18 Jan 2007	5.90	capture		07 Oct 2007	262	N
13 Mar 2008	7.05	capture		No histology data		
22 May 2008	7.24	capture		No histology data		
22 Aug 2008	7.49	capture		07 Aug 2008	15	N
22 Sep 2008	7.58	capture		11 Sep 2008	11	N
29 Sep 2008	**7.60**	**capture**		**02 Oct 2008**	**3**	**Y**
06 Oct 2008	**7.62**	**capture**		**09 Oct 2008**	**3**	**Y**
14 Oct 2008	**7.64**	**capture**		**16 Oct 2008**	**2**	**Y**
20 Oct 2008	**7.66**	**capture**		**23 Oct 2008**	**3**	**Y**
27 Oct 2008	7.67	capture		23 Oct 2008	4	N
25 Nov 2008	**7.75**	**capture**		**27 Nov 2008**	**2**	**Y**
21 Apr 2009	8.16	capture		16 Apr 2009	5	N
04 Sep 2009	8.53	end of dental development				

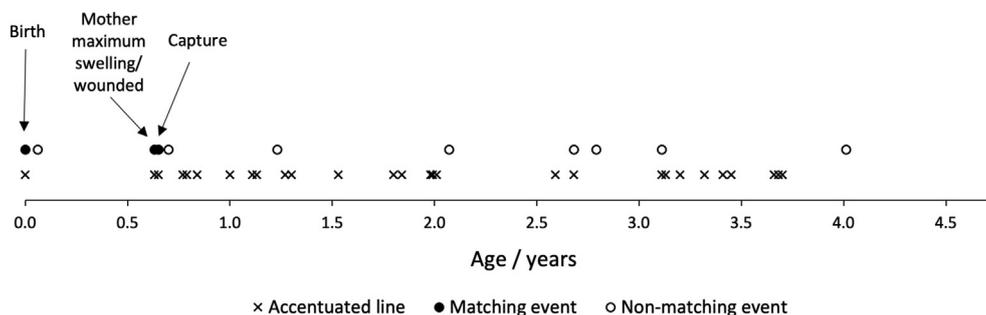[a] '?' indicates where we don't know the date of an event.

Figure 6. Accentuated lines in the dentition of 17E2. Matching events occurred within 3 days of a line and are labeled. Non-matching events are not labeled. The x-axis ends at 4.76 years after which the quality of the section was too poor to assess.

Table 6
Dates and ages at which events occurred in the life of mandrill 17E2, with the date of the closest accentuated line that formed in her dentition and whether we considered it a match. Bold indicates lines with a match (i.e., the line formed within ±3 days of the event).

Date	Age (years)	Own life event	Mother's life event	Date closest accentuated line	Days between event and accentuated line	Considered a match?
17 Feb 2002	**0**	**birth**		**17 Feb 2002**	**0**	**Y**
11 Mar 2002	0.06	capture		17 Feb 2002	22	N
07 Sep−02 Oct 2002	**0.55−0.58**		**inflating swelling**	**05 Oct 2002**	**3−28**	**Y**
02 Oct 2002	**0.62**		**wounded**	**05 Oct 2002**	**3**	**Y**
03−06 Oct 2002	**0.62−0.63**		**maximum swelling**	**05 Oct 2002**	**0−3**	**Y**
10 Oct 2002	**0.63**	**capture**		**13 Oct 2002**	**3**	**Y**
31 Oct−09 Nov 2002	0.70−0.73		inflating swelling, did not reach maximum	13 Oct 2002	18−27	N
12 May 2003	1.23	capture		24 May 2003	12	N
10 Mar 2004	2.07	capture		22 Feb 2004	17	N
22 Oct 2004	2.68	capture		27 Oct 2004	5	N
Dec 2004	2.79−2.87	alpha male change		27 Oct 2004	35−65	N
23 Mar 2005	3.11	capture		29 Mar 2005	6	N
18 Feb 2006	4.01	capture		16 Nov 2006	271	N
09 Sep 2011	8.34	died		n/a	n/a	n/a

formed an accentuated line the second time her mother was mate-guarded (but not the first, or during subsequent cycles). The proximity of large males and intermale aggression during mate-guarding may increase the offspring's stress levels, comparable to 'spectator stress' (Sapolsky, 2004; Jackson, 2013). 17E2's mother was not mate-guarded but was wounded during her first swelling cycle after his birth. This event is likely to have been stressful to her offspring, and 17E2 formed an accentuated line that matched this event.

5D3A formed a line to match the birth of her first sibling, but not her second, PB did not form a line to match the birth of PC and formed a line 6 days after the estimated birth of PD, and 17E2 had no siblings. Like the resumption of cycling, sibling birth is likely associated with reduced maternal care, which can increase offspring distress (Bowlby, 1969; Trivers, 1974; Devinney et al., 2001, 2003). This is likely to be particularly the case when the first sibling is born, when an individual is still reliant on maternal support and has not experienced the presence of a younger sibling before. This may explain why 5D3A formed an accentuated line when her first sibling was born, but not when her second sibling was born. However, if anything, PB showed the reverse pattern: she did not form an accentuated line when her first younger sibling was born but may have done when her second sibling was born. These findings suggest that the stress associated with sibling birth varies. Our findings that the mother's resumption of cycling is more reli-ably associated with accentuated lines than the birth of siblings reflect studies showing that maternal care decreases more

intensely when mothers resume cycling than when the next offspring is born (Berman et al., 1994; Devinney et al., 2001; Schino and Troisi, 2001).

One female (PB) formed accentuated lines during her first sexual swelling cycle, when she conceived her first offspring. In fact, the accentuated lines associated with PB's first sexual swellings were particularly marked, uniform in all teeth forming at the time and were the main connecting point when matching her teeth to study her dental development. PB also formed a line when we inferred she had a further sexual swelling cycle and know she conceived her second offspring. PB was not mate-guarded by males. The other female (5D3A) formed an accentuated line that matched the very end of her first sexual swelling cycle and was within 4 days of her maximum swelling when she was mate-guarded by a male (our criterion for a match was 3 days). 5D3A then experienced an abortion at some point during a 15-week period, and also formed two accentuated lines during this time, but we do not have accurate information to know if these matched the abortion. When 5D3A cycled again, a line matched her maximum swelling and 4 days of mate-guarding. Together, these findings suggest that some sexual swelling cycles (2/2 for PB, 1/2 for 5D3A) and mate-guarding (1/2 cases for 5D3A) are related to accentuated lines, and in the case of PB's first cycle very strong lines, but others are not. Menarche and subsequent cycles are linked to physiological changes in the body of female primates which may affect the formation of accentuated lines (Dixson, 2012; Plant and Zeleznik, 2015). They are also linked to important social changes. Females with sexual swellings are in

much closer contact with much larger males than they are at other times. Mate-guarding, in particular, is likely to be costly for females (Smuts and Smuts, 1993; Palombit, 2014). Thus, both physiological and psychological aspects of sexual swelling cycles are likely to stimulate the formation of accentuated lines, throughout the sexual swelling and at the time of mate-guarding. Together, our findings partially support the hypothesis that females form accentuated lines during their first and subsequent menstrual cycles (Dirks et al., 2002).

All three parturitions experienced by the two females in our study matched accentuated lines in their teeth. These results reflect findings in rhesus macaques (Cerrito et al., 2021) and in other mammals, although markings in those teeth accounted for the minimum number of parturitions rather than accurately recording every parturition that took place (Okada, 1943; Klevezal and Myrick, 1984; Trunova et al., 1999). The physiological events surrounding parturition and the many transient shifts in blood chemistry that might affect accentuated line formation at this time are likely to be very complex, but since calcium deposition is clearly disrupted in dentine (Dean and Elamin, 2014), it is likely to also be disrupted during enamel formation.

Perhaps surprisingly, no lines formed when PB's first infant was euthanized. Loss of an infant affects primate behavior (e.g. Biro et al., 2010; Anderson, 2011; Gonçalves and Carvalho, 2019) and female mandrills may carry the body of a dead infant for days (Setchell, pers. obs; Lemmers, pers. obs.), as in other primates (Biro et al., 2010; Carter et al., 2020). However, primiparous female mandrills often appear to be stressed by the continuous presence of an infant, and those that lose an infant return to playful, juvenile-like behavior immediately (Setchell, pers. obs.), suggesting that PB's stress levels may have reduced, rather than increased, with the loss of her infant.

4.2. Changes in alpha male

Changes in alpha male matched the formation of accentuated lines in our study subjects' teeth in only two cases (1/4 for PB, 1/6 for 5D3A, 0/1 for 17E2; overall 2/11). This suggests that (most) changes in alpha male did not affect the individuals in our study sufficiently to disrupt dental development. This may reflect the life history stages of our subjects. Changes in alpha male are expected to be particularly stressful for other animals if they endanger that animal's life, their infant's life, or their position in a group. For example, infanticide theory holds that infants are in danger of being killed if they are not sired by the new alpha male (Hrdy, 1979). A change in alpha male may therefore be stressful for a pregnant female, if the infant will be at risk of infanticide when it is born. In geladas (*Theropithecus gelada*), where one male dominates reproduction in a unit, 80% of pregnant females miscarry shortly after changes in dominant male (Roberts et al., 2012). In our study, a change in alpha male coincided with one of the four pregnancies in our female subjects and this was the only time a female (5D3A) formed a line to match a change in alpha male. She subsequently aborted the pregnancy. While paternity is highly concentrated on the alpha male in mandrills (Charpentier et al., 2005; Setchell et al., 2005b), mandrills are polygynandrous, unlike geladas, and sexual swelling records suggest that spontaneous termination is uncommon in the CIRMF mandrill colony. Thus, it seems unlikely that females often abort pregnancy in response to a change in dominant male.

A lactating female might also be affected by a change in alpha male since she is at risk of losing an infant (Hrdy, 1979; van Schaik and Janson, 2000; Engh et al., 2006). In line with this, female baboons who are at risk of infanticide show elevated levels of glucocorticoids (hormones associated with a stress response) during alpha male changes, but females who had no infant to protect do not (Beehner et al., 2000; Bergman et al., 2005; Engh et al., 2006). This suggests that lactating females are more likely to form accentuated lines when the alpha male changes than other females are. Neither of the female mandrills was lactating during any of the changes in alpha male in our study, which might contribute to the absence of accentuated lines at these times.

The one change in alpha male that did coincide with formation of an accentuated line in PB's teeth took place within nine weeks of another change in alpha male. The short timeframe in which these two changes took place suggests a high degree of male conflict and social instability during these weeks. If this is true, then the way a change in alpha male takes place and the amount of social instability during to a transition period may be correlated with the formation of accentuated lines, since more accentuated lines formed during a prolonged period of social instability than during single changes in alpha male.

Turning to our male subject, 17E2 was a juvenile not yet 3 years old when the alpha male changed in his group. He had not yet undergone puberty, so was not competing for rank and access to receptive females. The change in alpha male might have had few implications for a juvenile male and thus may not have stimulated a stress-response leading to accentuated line formation.

4.3. Captures

Captures did not match consistently with the formation of accentuated lines (2/13 captures for PB, 6/18 for 5D3A, 1/7 for 17E2; overall 9/38). This result is unexpected, as previous studies showed that captures, transfers, hospitalization and possibly anesthesia may match with accentuated line formation (Bowman, 1991; Schwartz et al., 2006; Austin et al., 2016). Individuals may habituate to captures, which may become less stressful over time (Creel, 2001; Sapolsky, 2004). The specific capture circumstances may also influence accentuated line formation. When female 5D3A was caught multiple times over a short period in late 2008, several of these captures co-occurred with accentuated lines, suggesting this period was stressful for her. Additionally, our results show that the administration of an anesthetic is not sufficient to consistently result in the formation of accentuated lines. The dose of anesthetic varies during CIRMF captures, and the amount of anesthetic applied, how efficiently the capture is conducted, and how much psychological stress an individual experiences before being sedated may all affect line formation.

4.4. Broader implications for inferring specific stress events in paleobiology

Our results showing a correlation between accentuated line formation and life history events suggest that the study of accentuated lines may be useful in reconstructing life history trajectories in extinct species. Our fine-grained data on the timing of life history events reveal that sometimes lines form in the teeth that correspond to the timing of these events while at other times they do not. Interestingly, our single male individual's pattern of accentuated lines was very different from those of the two females. Our small sample precludes understanding sex or rank differences in accentuated line formation and a larger sample might help shed light on how different individuals respond to stress. Nevertheless, our demonstration that accentuated line formation at the time of life history events is unlikely to be due to random chance provides a very useful advance in understanding how stress is recorded in dental tissues.

Further tests of the relationships we examine using a large sample of animals of known life history are needed to extend our

findings, but such studies are a daunting prospect given the time-consuming nature of the methodology. One possibility is to focus analyses on teeth forming at the time of a specific event. For example, although species vary in the timing of life history events relative to dental development (Dirks and Bowman 2007), our data suggest that it would be possible to focus on the M1 when examining resumption of the mother's cycle as a proxy for weaning in papionins. Studies of accentuated lines could also be aided by rapid and nondestructive data acquisition using phase-contrast synchrotron radiation microtomography (Tafforeau and Smith, 2008).

In addition to the accentuated lines that matched particular life history events, many other lines formed in the teeth of our study animals that do not match a recorded event. These unmatched lines may be independent of stressful events, but, given the link between lines and metabolic disturbance, it seems more likely that they match physiologically stressful events that are not captured in the life history events we were specifically interested in. In addition to the events we recorded, many other events are likely to result in physiological stress to the mandrills, including social stress (Silk, 2002). The CIRMF mandrills spend a substantial proportion of their time in the densely forested parts of their enclosures, limiting behavioral observations to a few hours per day, meaning that many events are hidden to the observer. Monitoring glucocorticoid metabolite levels in fecal samples can provide a noninvasive record of HPA axis activation (Hodges and Heistermann, 2011). However, collecting regular samples across the period of tooth formation (up to age 6.5 years in females, and 9 years in males in these mandrills, Dirks et al., 2020), or a shorter specific period of interest (e.g. around weaning) would require a concentrated sampling effort, followed by (we hope) a long wait before the animal died a natural death, and the teeth could be recovered.

The occurrence of accentuated lines that are unrelated to observed life history events suggests that accentuated line assessment should be combined with other methods, such as trace element analysis, if we are to use it to reconstruct primate paleobiology. Work by Humphrey and colleagues (Humphrey et al., 2007, Humphrey et al., 2008a, b; Humphrey, 2008) has shown that changes in strontium/calcium ratios in enamel track dietary shifts during weaning. Based on a study of baboons of unknown life history, Dirks et al. (2010) suggested that the shift in suckling frequency resulting in the mother's return to cycling matched accentuated lines in a female baboon but not a male. Trace element analyses have been used to document age at weaning in hominin teeth, but without analyses of accentuated line formation (Austin et al., 2013; Joannes-Boyau et al., 2019; Nava et al., 2020), although one study found an association between barium banding in enamel and an accentuated line in a Neanderthal tooth (Smith et al., 2018). A study combining accentuated line formation and trace element analysis in a larger sample of extant primates of known life history, both within and across species, would advance our understanding of the links between life history events and accentuated lines. It would also be of great interest to understand whether life history trade-offs during weaning caused similar degrees of physiological stress in extinct hominins to those we have demonstrated in mandrills.

5. Conclusions

We determined the ages at formation of accentuated lines in the teeth of male and female mandrills and tested the hypothesis that stress associated with specific life history events affects tooth formation, and therefore matches the formation of accentuated lines in tooth sections. Resumption of the mother's sexual swelling cycle and mate-guarding by males coincided with the formation of accentuated lines in two animals. One individual formed an

accentuated line that coincided with the birth of one sibling, but not that of another sibling. In the two female mandrills, all but one of their sexual swelling cycles and one of two cases of mate-guarding matched accentuated lines, and in one case a female's first cycle matched very strong lines in her teeth. All three parturitions in the two females coincided with the formation of accentuated lines. We further compared our histological data with the timing of changes in alpha male and captures of the mandrills by the CIRMF staff. Changes in alpha male and captures did not consistently coincide with accentuated line formation, although repeated captures were associated with lines. Finally, we advance studies of the relationship between tooth formation and life histories by using simulations to compare our results to chance expectations. We found that the number of observed matches would be very unlikely if accentuated tooth line formation is unrelated to the timing of life history events. Our results show that life history events, which are part of the normal life cycle, can be sufficiently physiologically costly to affect ameloblast function and leave a record of accentuated line formation in teeth. These results provide more robust evidence that accentuated tooth line formation is associated with the timing of stressful life events than previous studies.

Supplementary Online Material

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