

Elemental models of primate nursing and weaning revisited

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Funding information

Australian Research Council, Grant/Award Numbers: DP210101913, FT200100390; Eunice Kennedy Shriver National Institute of Child Health & Human Development of the National Institutes of Health, Grant/Award Number: R00HD087523; Icahn School of Medicine at Mount Sinai

Abstract

Objectives: Intra-tooth patterns of trace elements barium (Ba) and strontium (Sr) have been used to infer human and nonhuman primate nursing histories, including australopithecine and Neanderthal juveniles. Here, we contrast the two elemental models in first molars (M1s) of four wild baboons and explore the assumptions that underlie each.

Materials and Methods: Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) was employed to create comprehensive calcium-normalized barium and strontium (Ba/Ca, Sr/Ca) maps of M1 enamel and dentine at 35 micron resolution.

Results: Postnatal Ba/Ca values were typically high, peaking ~0.5 years of age and then decreasing throughout M1 crown formation; all four individuals showed minimal Ba/Ca values between ~1.2–1.8 years, consistent with field reports of the cessation of suckling. Enamel Sr/Ca did not support patterns of previous LA-ICP-MS spot sampling as the enamel rarely showed discrete Sr/Ca secretory zonation. Increases in Sr/Ca appeared in coronal dentine beginning ~0.3 years, with varied peak value ages (~0.7–2.7 years) and no evidence of a predicted postweaning decline.

Discussion: Inferences of baboon weaning ages from initial Ba/Ca minima are more congruent with behavioral observations than Sr/Ca maxima; this is consistent with studies of captive macaques of known weaning ages. Elemental variation is more apparent in the coronal dentine than the enamel of these baboons, which may relate to its more rapid mineralization and protection from the oral environment. Inferences of nursing histories from enamel Sr/Ca patterns alone should be reconsidered, and elevated values of Ba/Ca and Sr/Ca in teeth formed after weaning require further study.

KEYWORDS

barium, milk, strontium, tooth chemistry, trace elements

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1 | INTRODUCTION

The consequential process of infant nursing—including the provisioning of maternal milk, progressive consumption of supplemental solid foods, and cessation of suckling at weaning—is recorded in the chemistry of concurrently forming teeth. Dental studies of nursing in human prehistory have conventionally relied on isotopic ratios measured from drilled samples, serial sections, or biopsy punched-samples (reviewed in Tsutaya & Yoneda, 2015; Pederzani & Britton, 2019), although each individual measurement conflates months of tooth formation and yields broad, coarsely-timed estimates of nursing behavior (Czermak et al., 2020; Tsutaya, 2020). More recently, scholars have employed laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) to infer nursing behavior from trace element ratios in human and nonhuman primate teeth (reviewed in Clark et al., 2020; Smith et al., 2021). An advantage of this approach is its much finer scale—allowing discrete measurements to be related to incremental dental development, and yielding potentially more precise estimates of transitions throughout nursing.

Building on a study of bone chemistry by Sillen and Smith (1984), Humphrey and colleagues explored nursing behavior in sectioned tooth enamel from distributions of the non-essential trace element strontium (Sr) relative to calcium (Ca) (Humphrey et al., 2007; Humphrey, Dean, et al., 2008; Humphrey, Dirks, et al., 2008). This creative approach leveraged knowledge of microscopic growth to provide a temporal framework for Sr/Ca concentration changes measured from a series of discontinuous 30 μm -diameter laser spots of human and baboon tooth enamel. Results from two wild baboons were employed to formulate an elemental model identifying the introduction of non-milk supplemental foods (initial increase in Sr/Ca) and the transition to an adult diet at the cessation of suckling (peak Sr/Ca; Humphrey, Dirks, et al., 2008: Fig. 1, p. 201). They stated that postweaning Sr/Ca values should then fall from this peak due to decreasing Sr absorption by the gastrointestinal tract, noting that periodic fluctuations in Sr/Ca might appear in later forming enamel due to seasonally limited foods. Austin et al. (2013) then studied nursing from Ca-normalized distributions of the non-essential element barium (Ba) in human, macaque, and Neanderthal teeth, finding more consistent and pronounced transitions in Ba/Ca relative to Sr/Ca for individuals of known histories. It was observed that Ba/Ca rises with the intensification of nursing and falls to prenatal levels once milk intake ends; the physiological basis of this model is explained in detail in Smith et al. (2021, 2022) and illustrated in Smith et al. (2021: Fig. 2, p. 6.). Importantly, the amount of Ba and Sr differs markedly relative to Ca such that elevated Ba/Ca is a demonstrable marker of milk intake, which is thought to be the converse situation for Sr/Ca (i.e., elevated Sr/Ca comes from nonmilk foods).

Following on the first reconstruction of nursing transitions in a Neanderthal (Austin et al., 2013), scholars have since measured Ba/Ca and Sr/Ca in sectioned australopithecine, Neanderthal, and buried modern human teeth for insights into ancient childrearing practices (Joannes-Boyau et al., 2019; Nava et al., 2020; Smith et al., 2018). The choice of element is not without debate; we have argued that

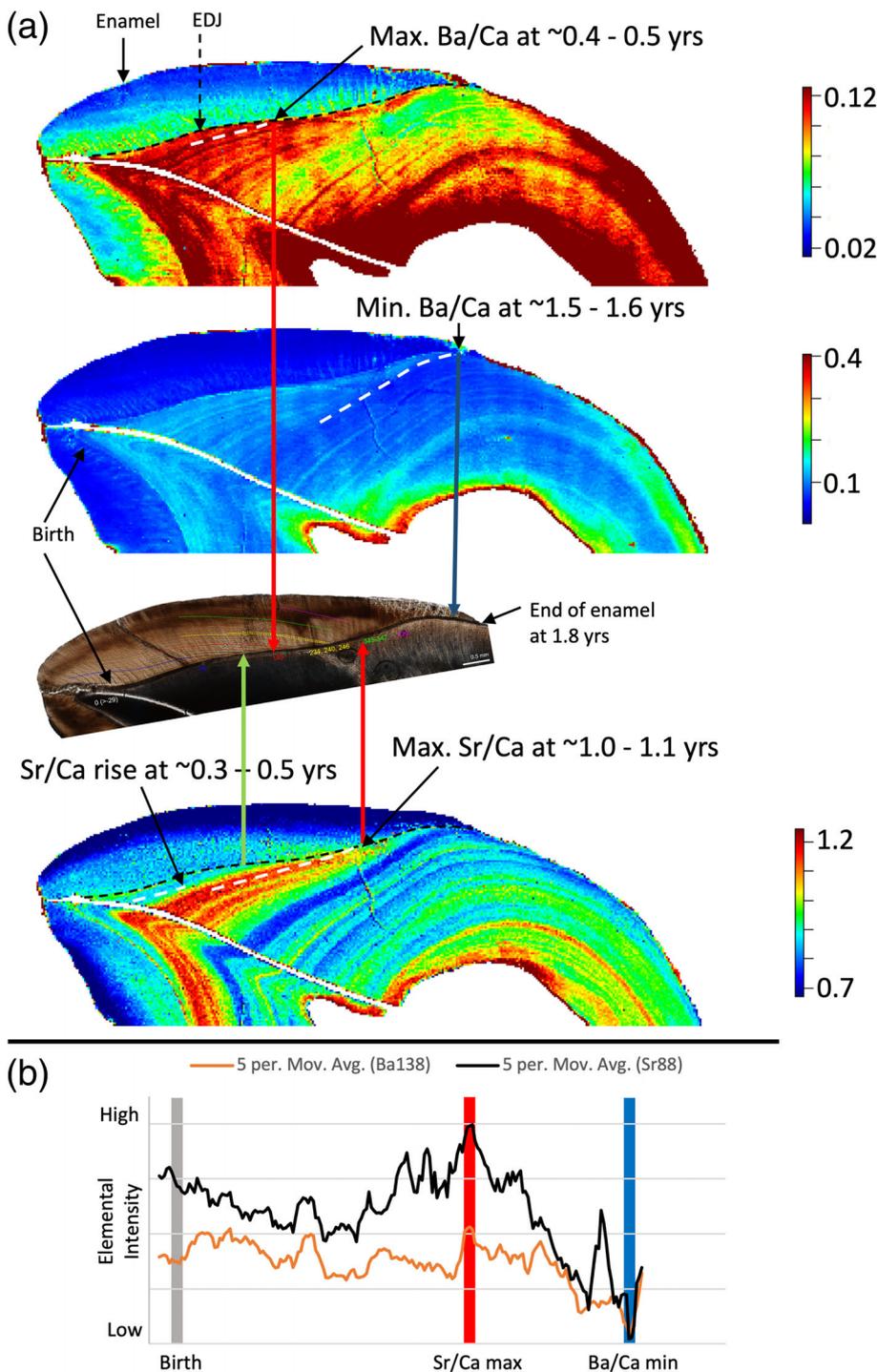
Ba/Ca measurements are more informative about the initiation and duration of suckling (e.g., Austin et al., 2013; Smith et al., 2021, 2022), while others have suggested that Sr/Ca distributions are more accurate (e.g., Li et al., 2020; Müller et al., 2019; Nava et al., 2020). Such explorations have also been extended into other mammals; Clark et al. (2020) conducted an elemental study of early-formed walrus teeth, revealing Ba and Sr decreases that are consistent with the Ba/Ca nursing model developed by Austin et al. (2013) but inconsistent with the Sr/Ca model proposed by Humphrey, Dirks, et al. (2008). Funston et al. (2022) documented nursing transitions from Ba-rich regions in the molars of a 62 million-year-old pantodont, providing key insight into this enigmatic placental mammal.

Here, we provide further clarification by measuring Ba/Ca and Sr/Ca in first molars (M1s) of the two Ugandan baboons studied by Humphrey, Dirks, et al. (2008), as well as two additional juvenile baboons from Ethiopia. Elemental maps from continuous 35 μm linear sampling of the coronal enamel and dentine (as well as the root dentine) provide a more comprehensive perspective than discrete spot samples or singular linear traces of enamel alone. This line-ablation method also yields better signal stability and higher count rates than spot samples (Speakman & Neff, 2005). A further advantage of our LA-ICP-MS approach is that serial-forming teeth can be registered by matching concurrent elemental bands (Smith et al., 2017, 2021)—permitting a reappraisal of these four individuals' ages at death, as well as an initial assessment of postweaning elemental patterns.

2 | MATERIALS AND METHODS

We employed the histological sections of mandibular M1s of the four baboons from Dirks et al. (2002): Ugandan *Papio anubis* individuals U9 and U10, and Ethiopian *Papio hamadryas-anubis* hybrid individuals 73261 and 73436. An additional histological section was prepared for the distal M1 cusps of U9, which was required due to planar obliquity of the available M1 section (Smith et al., 2022). Studies of enamel Sr/Ca via LA-ICP-MS spot samples and developmental stress in the two Ugandan baboons (U9, U10) have been conducted by Humphrey, Dirks, et al. (2008) and Dirks et al. (2010), and perinatal transitions in Sr/Ca and Ba/Ca have been assessed for all individuals (Smith et al., 2022).

Crown formation times and ages were determined by methods detailed in Smith et al. (2022). In brief, neonatal lines were first located in the cuspal enamel through observation with an Olympus BX 51 polarizing light microscope using a range of objectives ($\times 10$, $\times 20$, $\times 40$) and variable illumination with partially and fully polarized light. Images were captured with an Olympus DP 73 camera and CellSens software, and low-resolution ($\times 4$ objective lens) montages were made with Adobe Photoshop and Microsoft Photodraw in order to identify and annotate accentuated lines in the enamel (Figure S1). We established the timing of these temporal maps by working from the earliest formed enamel over the dentine horn (or worn occlusal edge) to the enamel cervix as follows. The length of enamel prisms between the dentine horn tip and an accentuated line



was measured and divided by the daily secretion rate (determined from the spacing of local daily cross-striations measured with a $\times 40$ objective lens), which was then repeated for sequential regions along the EDJ (separated by accentuated lines) until the enamel cervix was reached (following the method in Boyde, 1963: Figs. 2 and 3). In the lateral enamel formation times were sometimes determined by multiplying the number of local long-period lines between accentuated lines by the individual's periodicity (number of daily increments between serial long-period lines). Formation times of serial segments along the EDJ were summed to yield cusp-specific formation times,

and prenatal formation times were subtracted to yield sequential ages (Figure S1). The two Ethiopian individuals show marked wear, and cuspal enamel in U9 is cracked, leading to slight underestimates of prenatal enamel and total formation times.

All teeth were subject to comprehensive linear LA-ICP-MS mapping as in Smith et al. (2022), and multiple visual outputs were rendered to optimize element/Ca ratio gradients in enamel and dentine (e.g., upper and middle Ba/Ca maps in Figure 1). Elemental maps were produced with a New Wave Research NWR-193 laser ablation system connected to an Agilent Technologies 8800s inductively coupled plasma-mass

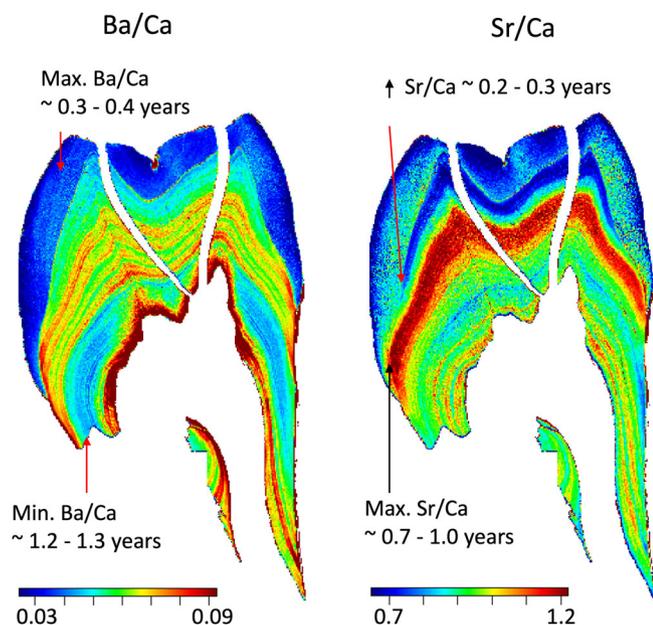


FIGURE 2 Elemental maps of the M_1 of *Papio anubis* U10. See Figure 1 for explanation of color scales and interpretative method

spectrometer (ICP-MS). A 35 μm diameter aperture was inserted in the laser beam as it rastered along sample surfaces in parallel straight lines, producing adjacent data points that correspond to a pixel size of approximately $35 \times 35 \mu\text{m}$. Data were analyzed as metal to Ca ratios (e.g., $^{138}\text{Ba}/^{43}\text{Ca}$, $^{88}\text{Sr}/^{43}\text{Ca}$) to compensate for variation in the mineral content between samples. Images were rendered with custom software (detailed in Niedzwiecki et al., 2016), and element/Ca ratios rather than concentrations are provided as matrix-matched standards are not available (detailed further in Smith et al., 2021). Visual representations of element/Ca ratios in Figures 2–4 were selected to optimize the contrast of enamel, which often shows more subtle patterns of variation than more rapidly mineralizing dentine, by adjusting the minimum and maximum of the color scales. The distal M_1 section from U9 was subject to LA-ICP-MS prior to polishing and cover slipping, leading to subtle linear artifacts in Ba/Ca that are not evident in the polished section mesial section shown in Smith et al. (2022), in addition to artificially elevated values in the cervix (Figure 1).

Elemental trends are assessed progressively from the earliest forming region (dentine horn tip) to the enamel cervix along the enamel-dentine junction (EDJ) with direct reference to temporal maps. Elemental transitions were aged by alignment of elemental maps with temporal overviews of the four teeth (Figure 1), and transitions that occurred between accentuated lines were timed through measurements of EDJ distances divided by local extension rates (previously determined for each segment along the EDJ as distance divided by formation time). We registered the M_1 root to the upper canine by matching elemental maps in one instance (U10), and aged root dentine from long-period lines in another case (73261; Figure S1). Age at death was determined for each individual by matching elemental bands in M_1 s to concurrently-forming teeth (illustrated for Ethiopian baboon 73436 in Smith et al., 2021: Fig. 4, p. 9), and

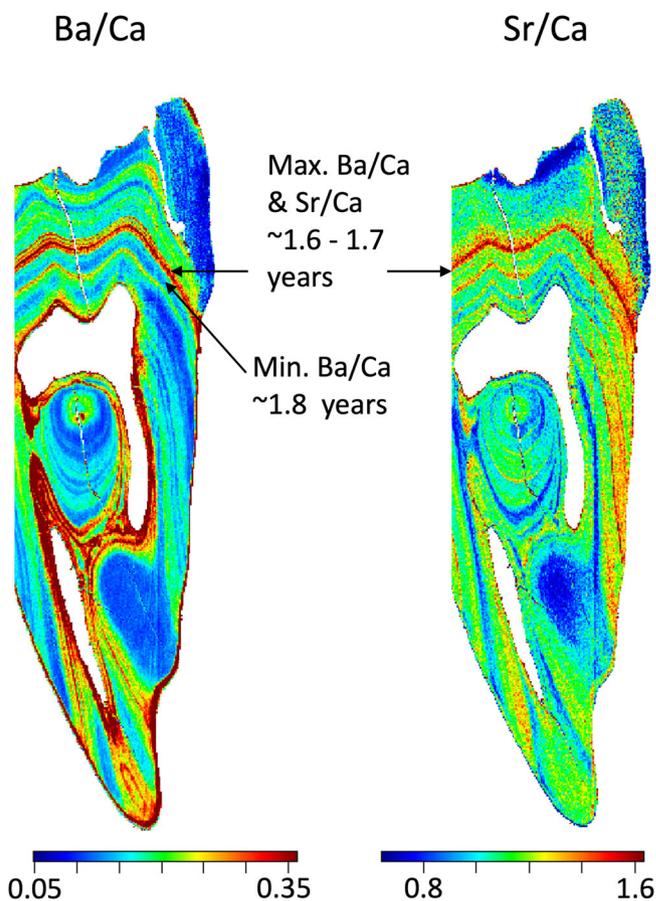


FIGURE 3 Elemental maps of the worn M_1 of *Papio hamadryas-anubis* hybrid individual 73261. See Figure 1 for explanation of color scales and interpretative method

continuing cumulative assessments of developmental time as detailed above until the end of tooth formation at death was reached. Below we detail results relevant to the Austin et al. (2013) Ba/Ca nursing model predictions (maximum value = peak milk intake; minimum value = cessation of milk intake) and the Humphrey, Dirks, et al. (2008) Sr/Ca model (initial postnatal rise = initiation of solid-food consumption; maximum value = cessation of milk intake) for each individual baboon.

3 | RESULTS

Long-period line periodicities, prenatal formation times, cusp-specific crown formation times and ages, and approximate ages at death are given in Table 1. Ugandan individual U9 reaches a Ba/Ca maximum at ~ 0.4 – 0.5 years of age followed by a slow decline, and minimum values beginning at ~ 1.5 – 1.6 years (Figure 1). After crown formation, Ba/Ca remained relatively low save for one wide band in the middle of the root (and along the pulp chamber). This individual shows an increase in Sr/Ca beginning at ~ 0.3 – 0.5 years of age that peaks at ~ 1.0 – 1.1 years, eventually reaching a minimum at ~ 1.5 – 1.6 years. The root dentine formed after the crown reveals several rises and falls in Sr/Ca

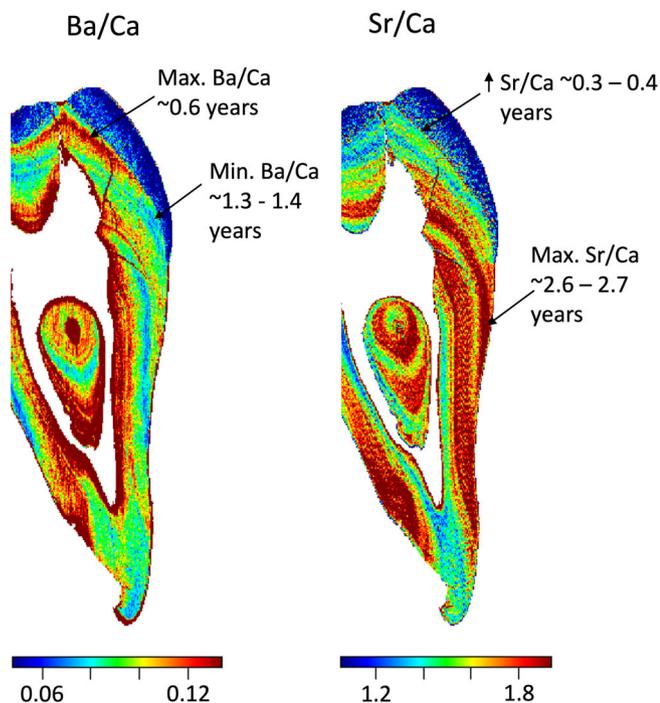


FIGURE 4 Elemental maps of the worn M₁ of *Papio hamadryas-anubis* hybrid individual 73436. See Figure 1 for explanation of color scales and interpretative method

over the next few years. Overall, the coronal enamel and dentine show broadly similar elemental transitions in U9, although Sr/Ca transitions are more evident in dentine.

Ugandan individual U10 shows different elemental patterns in the coronal enamel and dentine, which are detailed for each tissue individually. The enamel shows elevated Ba/Ca values for the first ~0.3–0.4 years of postnatal life followed by a slow decline for a few months, after which Ba/Ca values begin to rise until crown completion (Figure 2). The dentine shows a tiny cone of low (dark blue) prenatal Ba/Ca, followed by a rise until ~0.6 years of age, after which point four marked cyclical increases and decreases occur over the next 0.6 years, returning to minimum values beginning at ~1.2–1.3 years of age. A final broad elevated Ba/Ca band is apparent in the developing root shortly before death at ~2.4–2.6 years of age. The Sr/Ca patterns in enamel are largely indistinguishable along the EDJ throughout the year of postnatal formation. In contrast, the coronal dentine shows several zones of changing Sr/Ca ratios, with elevated values

from ~0.2–0.3 years of age until a peak at ~0.7–1.0 years of age, a decrease until ~1.2 years of age, and then three brief rises and falls prior to death.

Ethiopian baboon 73261 is more challenging to interpret due to M1 attrition, a crack in the underlying dentine, and likely post-eruptive modification of the outer enamel and exposed dentine—which show elemental patterns that do not conform to the geometry of growth increments (Figure 3). Enamel shows patchy elevated Ba/Ca values for the first several months of postnatal life followed by a brief decline, after which Ba/Ca values begin to rise until crown completion. Coronal dentine shows clearer Ba/Ca zonation, with a progressive increase until ~0.7 years of age (fine red band below the crack), followed by a brief decrease, then an increase until ~1.6–1.7 years of age, returning to minimum values for several months beginning at ~1.8 years of age. Enamel Sr/Ca patterns are largely indistinguishable along the EDJ throughout the 1.3 years of postnatal formation. Dentine shows several Sr/Ca zones that are difficult to time, with values increasing until ~1.6–1.7 years of age, followed by cyclical decreases and increases in the root.

Ethiopian baboon 73436 shows Ba/Ca increasing until a peak at ~0.6 years of age in enamel and dentine, followed by a decrease to minimal values at ~1.3–1.4 years that is more apparent in the coronal dentine (Figure 4). The root dentine shows two additional prolonged rises and falls of Ba/Ca long after nursing is likely to have ended. Enamel Sr/Ca patterns are again largely indistinguishable along the EDJ throughout 1.7 years of postnatal formation, while the coronal dentine shows an initial increase at ~0.3–0.4 years of age for several months, followed by a decrease, and then a gradual rise culminating in a sustained peak beginning at ~2.6–2.7 years of age (coincident with elevated Ba/Ca), and additional cyclical variation.

4 | DISCUSSION

4.1 | Comparisons to previous histological and elemental studies

This analysis yields several differences relative to results reported in Humphrey, Dirks, et al. (2008) and Dirks et al. (2002). Two baboons' periodicities were revised down from 7 to 6 days (U10, 73261), M1 crown formation times of U9 and 73436 increased by several months, and ages at death increased for all individuals save for U10. Elemental

TABLE 1 Demographic and developmental variables for the four baboons

Baboon	Sex	M1 cusp	Periodicity (days)	Prenatal (days)	CFT (days)	Age CC (days)	Death (years)
U9	M	db	7	>29	>689	660	~4.6–5.0
U10	F	mb	6	45	428	383	~2.4–2.6
73261	F	ml	6	>43	>535	492	~8–9
73436	F	mb	7	>48	>676	628	~6.3–6.5

Note: Sex: M = male, F = female; M1 Cusp: db = distobuccal, mb = mesiobuccal, ml = mesiolingual; Periodicity: number of days between long-period lines; Prenatal: time prior to formation of neonatal (birth) line; CFT: crown formation time (cusp-specific); Age CC: age at crown completion.

TABLE 2 Elemental patterns observed in the M1s of the four baboons (in years)

Baboon	Ba/Ca max	Ba/Ca min	Sr/Ca increase	Sr/Ca max
U9	~0.4–0.5	~1.5–1.6	~0.3–0.5	~1.0–1.1
U10	~0.3–0.4	~1.2–1.3 ^a	~0.2–0.3	~0.7–1.0
73261	~0.7 ^b	~1.8	≥0.3	~1.6–1.7
73436	~0.6	~1.3–1.4	~0.3–0.4	~2.6–2.7

^aDetermined through elemental registration with upper canine bands.

^bSecond maxima at ~1.6–1.7 likely due to illness and/or dietary Ba as it is coincident with the initial maximum Sr/Ca values.

matching across concurrently forming teeth (illustrated for baboon 73436 in Smith et al., 2021: Fig. 4, p. 9) revealed several mismatches in previous microscopic accentuated line registrations, yielding older initiation ages for canines and posterior molars, and thus later ages at death. We also note that the ages of accentuated lines used to time elemental transitions in Humphrey, Dirks, et al. (2008) and Dirks et al. (2010) were determined from counts of daily lines made on low resolution photomontages of U9 and U10. Reassessment of their original U9 M1 mesiobuccal photomontage resulted in estimated daily secretion rates in excess of those later quantified from a different thin section of this same cusp with a $\times 40$ objective, which is due to insufficient resolving power of the objective lens used to create the original montages. In summary, the timing of Sr/Ca zones for U9 and U10 originally reported in Humphrey, Dirks, et al. (2008: Figs. 3 and 4, pp. 205 and 206) require revision, and thus cannot be directly compared to the results reported in this study.

Of greater consequence is the lack of evident Sr/Ca patterning in the enamel of three of four baboons, including baboon U10 studied by Humphrey, Dirks, et al. (2008). Observations of seemingly random Sr/Ca “noise” in the baboons’ inner enamel are consistent with diffuse enamel Sr/Ca patterns seen in captive macaque M1s (Austin et al., 2013; Smith et al., 2021), which are less structured than Ba/Ca patterns (a difference also observed for the Scladina Neanderthal M1 in Austin et al., 2013). This may be due to the fact that Sr is deposited more slowly in mineralizing tissues relative to Ba, likely due to its longer retention in the bloodstream (Panahifar et al., 2019). While Ba/Ca transitions are often more evident in the coronal dentine, they can still be discerned from the enamel of unworn teeth and well-preserved buried teeth (e.g., Austin et al., 2013; Smith et al., 2018, 2022)—permitting nursing inferences even when enamel maturation has obscured developmental trends in Sr/Ca.

4.2 | Implications for assessment of primate nursing

Reports of nursing behavior in baboons from southwest Uganda and the Ethiopian Rift are very limited. Rowell (1966) undertook a two-year study of *P. anubis* in Uganda’s Queen Elizabeth National Park, noting a postnatal “lactation interval of about five months” and that suckling continued until an infant was replaced by a new sibling at

approximately 1.0–1.3 years of age. This is consistent with our inference of intensive suckling in Ugandan individuals U9 and U10 until ~0.4 years of age from maximal enamel Ba/Ca values (Table 2). Nicolson (1982) reported that maternal rejection of suckling attempts peaked at 25–32 weeks in Kenyan *P. anubis*, just past our elemental estimate of peak lactation. She also reported that Kenyan *P. anubis* infants began nibbling grass at 1 month of age, rapidly increasing feeding bouts over the next few months, which is slightly younger than inferences of initial solid food intake from Sr/Ca increases beginning at ~0.3 years of age (Table 2).

Rowell’s (1966) estimates of cessation of suckling in Ugandan baboons are also broadly consistent with our trace element results from U9 and U10; Sr/Ca maxima yield ages of adult diet attainment by ~0.7–1.1 years, while Ba/Ca minima are reached at ~1.2–1.6 years. Ba/Ca ages are identical to observations of the cessation of suckling from other baboon populations (range 15–20 months: reviewed in Dirks et al., 2010), including a study of Kenyan *P. anubis* where it was reported that “no infant was completely weaned before 13 months of age and at least one infant was still suckling at 22.5 months” (Nicolson, 1982). Fewer reports of nursing behavior are available for Ethiopian *P. hamadryas*. Sigg et al. (1982) tracked individuals near Erer for nearly three years, reporting that mothers did not begin cycling for 10–16 months after the birth of a surviving infant, with interbirth intervals ranging from 18 to 28 months. This is consistent with weaning estimates from the two Ethiopian baboons’ minimal Ba/Ca values (~1.3–1.8 years), but less so for estimates from their maximal Sr/Ca values (~1.6–2.7 years). While we acknowledge that environmental and nutritional variation can impact baboon nursing behavior (e.g., Lycett et al., 1998), it is well established that wild baboon infants are weaned after their first year of life and before their third year begins.

Ethiopian baboon 73261 shows synchronous peaks in Sr/Ca and Ba/Ca at ~1.6–1.7 years of age that suggest the consumption of non-milk foods rich in both Ba and Sr (also see similar evidence for 73436 in Smith et al., 2021: Fig. S1). While elevated Ba and Sr may transiently appear in teeth after weaning in ailing captive macaques on uniform diets (Austin et al., 2016; Smith et al., 2021), we regard sustained rises in baboon Ba/Ca after the first ~0.5 years of life as due to the ingestion of Ba from dietary sources, soil, and/or dust. Thus, Ba may be more bioavailable from non-milk sources than was originally assumed by Austin et al. (2013), and there may be instances when a decrease in Ba/Ca due to the end of milk intake may be obscured by the absorption of concurrent dietary or environmental Ba.

Similarly, elevated Sr values can be found in wild primate dentitions long past the cessation of suckling, as seen in both Ethiopian baboons’ canines (Figure S2) and in great ape dentitions (Dean et al., 2018, 2020; Smith et al., 2021), calling into question assumptions about a postweaning decline of Sr absorption due to gastrointestinal tract maturation (Sillen & Smith, 1984). We are unaware of any longitudinal data from mineralized tissues that support this hypothesized decline; Sillen and Smith (1984) present cross-sectional data on Sr/Ca in humeri from an archeological population that are higher in

younger individuals than in older ones. However, children show multifactorial patterns of bone turnover (Szulc et al., 2000), humeral bone turnover rates are quite high (Fahy et al., 2017), and the chemistry of buried bone is commonly modified by the burial environment (Kohn & Moses, 2013). In their influential review, Sillen and Smith (1984) relied on the work of Lengemann (1963) and Rivera and Harley (1965) to identify weaning in a skeletal population; the latter study presented cross-sectional cadaveric Sr and Ca data from postindustrial American populations without controlling for dietary variation—yet the former established experimentally that Sr and Ca absorption decrease when either are increased in the diet. Thus, the effects of diet and age must be considered together, and longitudinal chemical records in primate teeth suggest that additional research is needed to decouple these factors.

Given the elemental patterns in baboons U10, 73261, and 73436, as well as the real likelihood of seasonal consumption of strontium-rich resources (reviewed in Dirks et al., 2010), it appears that elevated Sr/Ca patterns are not a reliable proxy for the cessation of suckling in baboons. In other words, the consumption of Sr-rich foods may vary during nursing and after nursing ends. This is perhaps most evident for baboon 73436, which did not show a peak Sr/Ca value until ~2.6–2.7 years of age—long past the point when baboon mothers resume reproductive cycling and typically birth a new infant. Additional evidence hints at a greater complexity of Sr/Ca than previously modeled; we have shown that Sr values can increase in the milk of captive macaques—close evolutionary relatives of baboons—despite their consumption of a uniform commercial diet (Austin et al., 2013). Furthermore, Glab et al. (2001) explored Sr in 54 teeth from nine wild baboons, and found higher Sr values in deciduous teeth primarily formed in utero and during exclusive suckling than in their M1s.

Recent studies that rely on changes in Sr/Ca to infer human and Neanderthal nursing histories (Li et al., 2020; Müller et al., 2019; Nava et al., 2020) would benefit from additional context about the seasonal bioavailability of Sr in non-milk foods and putative developmental changes in the absorption of this non-essential element. The methods used here to assess Ba/Ca and Sr/Ca are capable of measuring multiple elements within a single analysis without sacrificing sensitivity; such whole crown longitudinal approaches are likely to provide the most comprehensive perspective on infant dietary histories.

AUTHOR CONTRIBUTIONS

Tanya M. Smith: Conceptualization (lead); data curation (lead); formal analysis (equal); project administration (lead); writing – original draft (lead); writing – review and editing (equal). **Manish Arora:** Methodology (lead); resources (lead); writing – review and editing (supporting). **Maya Bharatiya:** Writing – review and editing (supporting). **Wendy Dirks:** Conceptualization (supporting); formal analysis (supporting); resources (supporting); writing – review and editing (supporting). **Christine Austin:** Formal analysis (equal); methodology (equal); resources (supporting); software (lead); visualization (lead); writing – review and editing (equal).

ACKNOWLEDGMENTS

The authors appreciate the considerable research assistance of Clifford Jolly and Donald Reid. This work was funded by the Australian Research Council (DP210101913, FT200100390), the Eunice Kennedy Shriver National Institute of Child Health & Human Development of the National Institutes of Health (R00HD087523), Griffith University, and the Icahn School of Medicine at Mount Sinai. The authors appreciate the suggestions of two reviewers and an Associate Editor, as well as editorial comments from Lulu Cook and Petra Vaiglova. Open access publishing facilitated by Griffith University, as part of the Wiley - Griffith University agreement via the Council of Australian University Librarians.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the figures and supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Smith, T. M., Arora, M., Bharatiya, M., Dirks, W., & Austin, C. (2023). Elemental models of primate nursing and weaning revisited. *American Journal of Biological Anthropology*, 180(1), 216–223. <https://doi.org/10.1002/ajpa.24655>