Erschienen in: American Journal of Physical Anthropology. Wiley-Blackwell. 2021, 176(4), pp. 684-691
https://doi.org/10.1002/ajpa.24376

In vivo deciduous dental eruption in LuiKotale bonobos and Gombe chimpanzees

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Funding information
Explorers Club; George Washington University; Leakey Foundation; Max-Planck-Institut für Evolutionäre Anthropologie; National Science Foundation, Grant/Award Numbers: BCS-1753437, BCS-1753651; Royal Zoological Society of Antwerp; Sigma Xi; Wenner-Gren Foundation

Abstract

Objectives: Existing data on bonobo and chimpanzee dental eruption timing are derived predominantly from captive individuals or deceased wild individuals. However, recent advances in noninvasive photographic monitoring of living, wild apes have enabled researchers to characterize dental eruption in relatively healthy individuals under naturalistic conditions. At present, such data are available for only one population of wild chimpanzees. We report data for an additional population of wild chimpanzees and the first dental eruption data for wild bonobos.

Materials and Methods: We collected photographs and video footage of teeth from the open mouths of wild bonobos and East African chimpanzees of known age from LuiKotale, Democratic Republic of the Congo, and Gombe National Park, Tanzania, respectively. We scored the presence and absence of deciduous teeth from photographs and video footage to characterize deciduous dental eruption timing in these two populations.

Results: Deciduous dental eruption ages in our sample fall within the range of variation previously documented for captive chimpanzees, but eruption ages are later in wild than in captive contexts. We found substantial variation in deciduous canine eruption timing, particularly among bonobos. One bonobo had a deciduous canine present by 227 days old while another did not have a deciduous canine present at 477 days old.

Discussion: Our data indicate that deciduous teeth erupt later in wild individuals than in captive individuals. We also found that deciduous dental eruption timing varies considerably between individuals within our study populations, a pattern that is consistent with previous studies. Future studies should consider sources of variation in deciduous canine eruption timing and relationships with other aspects of life history as additional data become available.

KEYWORDS
bonobos, chimpanzees, dental eruption, human evolution

1 | INTRODUCTION

Dental eruption is typically defined as the process of tooth movement from within the alveolar crypt to the fully occluded position in the dental arcade (Kuykendall et al., 1992; Nissen & Riesen, 1964). Early comparative studies highlighted covariance between dental eruption timing and life history milestones across a wide range of primates, most notably documenting an association between the timing of first permanent molar eruption and weaning (Godfrey et al., 2001; Smith, 1989, 1992). Thus, age at permanent tooth eruption, which can be calculated from incremental growth features in teeth of immature individuals, has been an important proxy for inferring hominin life history (e.g., Bromage & Christopher Dean, 1985; Kelley & Schwartz, 2012). However, other studies questioned the utility of extant great ape dental eruption timing for the purpose of inferring hominin life history (Kelley et al., 2020; Machanda et al., 2015; Smith et al., 2013; reviewed in Robson & Wood, 2008). Thus, there is a need for more data within narrower phylogenetic contexts, for example, within species and genera, to generate a better understanding of the relationship between dental eruption and life history milestones (see Kelley et al., 2020; Monson & Hlusko, 2018).

Until recently, information on dental eruption in our closest living great ape relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), was based predominantly on living or deceased captive individuals (Bolter & Zihlman, 2011; Conroy & James Mahoney, 1991; Kraemer et al., 1982; Kuykendall et al., 1992; Nissen & Riesen, 1964; Smith et al., 1994) or deceased free-ranging individuals of chronological age that was either known from living observations or determined from dental histology (Kelley et al., 2020; Smith & Boesch, 2011; Zihlman et al., 2004, 2007). Pusey (1978) described dental eruption observations in a small number of living, free-ranging chimpanzees from the Gombe East African chimpanzee population, and more recently, Smith et al. (2013) and Machanda et al. (2015) have pioneered methods to systematically document dental eruption timing in living, free-ranging chimpanzees. The method developed by Smith et al. (2013) and Machanda et al. (2015) entails photographing the open mouths of individually recognized animals with known life histories to evaluate their stage of dental eruption. This method has substantially improved our knowledge of dental eruption timing and its relationship to other life history variables in free-ranging chimpanzees. However, the studies by Smith et al. (2013) and Machanda et al. (2015) are based on one community of East African chimpanzees from the Kanyawara population. Additional data based on multiple populations and closely related species are needed to evaluate patterns of dental development in hominoids.

Here we report the presence/absence of deciduous teeth in living, wild bonobos from LuiKotale, Democratic Republic of the Congo and East African chimpanzees (*P. t. schweinfurthii*) from Gombe National Park, Tanzania. While most research has focused on permanent dental eruption timing, deciduous tooth eruption may be an important correlate of early infant development that reflects species differences in life history strategies and/or interindividual variation in developmental rates (Mahoney, 2019), given potential relationships between deciduous dental eruption and factors such as diet, body size, and/or phylogeny (Smith et al., 2015). We employed a photographic and video scoring method similar to that of Smith et al. (2013) and Machanda et al. (2015). Our results expand on the existing body of data on in vivo dental eruption in chimpanzees and provide the first such data in wild bonobos. These data thus provide critical benchmarks to compare to future and existing data on *Pan* dental eruption and further evaluate the utility of extant great ape dental eruption timing in hominin life history reconstruction.

2 | METHODS

2.1 | Study populations

We collected data on bonobos from the Bompusa East and Bompusa West communities at LuiKotale, Democratic Republic of the Congo. We collected data on chimpanzees from the Kasekela community at Gombe National Park, Tanzania. All bonobos and chimpanzees in our study were habituated to human observation. We focused our study on individuals younger than 2 years of age, as previous studies indicate that, in general, all deciduous teeth erupt during this period of infancy (e.g., Kuykendall et al., 1992). We determined the birthdate of individuals by taking the midpoint date between the date when the individual's mother was last observed without the newborn individual (hereon "earliest possible birthdate") and the date when the mother was first observed with the newborn individual (hereon "latest possible birthdate"). If the earliest and latest possible birthdates were consecutive dates, we assigned the birthdate as the latest possible birthdate. If the number of days between the earliest and latest possible birthdates was an even number of days, we used the later of the two midpoint dates. For all but one individual in our sample, the earliest and latest possible birthdates were separated by less than 24 days. For one bonobo, the earliest and latest possible birthdates were separated by 46 days. Therefore, the largest possible error associated with any individual's birthdate is 23 days. Our sample includes nine female bonobos, six male bonobos, three female chimpanzees, and four male chimpanzees.

2.2 | Photograph and video data collection

At LuiKotale, researchers following bonobos for behavioral data collection collected dental photographs of target individuals opportunistically between April 2014 and July 2017. At Gombe, researchers following chimpanzees for behavioral data collection began collecting dental photographs and video footage beginning in June 2013; this data collection is ongoing and data for this study include photographs and video footage until December 2019. At both study sites, photographs were collected using a high-resolution digital single-lens reflex camera and large aperture telephoto zoom lens. For dental photographs, we scored the presence/absence of teeth directly from the photographs (see next section). For video footage, we used Adobe Premiere to extract photographic stills from video footage when target individuals' teeth were scorable, that is, when one can clearly determine which teeth are present, then scored the presence/absence of teeth from these video stills as we describe below for photographs.

2.3 | Photograph and video still dental scoring

S.M.L and S.C.M. scored the presence or absence of all teeth from photograph and video still sessions; here, we define a session as one photograph or video still of a given individual or multiple photographs or video stills of a given individual taken on the same day. We used the following coding scheme to score teeth: Present = any part of the tooth crown is visible above the gumline (i.e., from the point of emergence of the cusp tip through the gingival margin, to full functional occlusion); Absent = the tooth is not visible (i.e., the cusp tips have not broken through the gumline); or Z = could not determine because the view of the tooth is obstructed (see e.g., Figure S1). We did not differentiate between the stage of eruption because we felt that Present/Absent was a less subjective metric given that some photographs and stills in our sample were difficult to score accurately beyond Present/Absent (e.g., very pixelated and/or dark). We viewed photographs in Adobe Photoshop and we adjusted image parameters (e.g., brightness) as needed to better assess tooth types and scores. S.M.L. and S.C.M. scored the full dataset by each scoring one subsample of the full dataset. S.M.L. and S.C.M. scored 41 of the same sessions to assess interobserver reliability. We calculated Cohen's Kappa in R version 4.0.2 (R Core Team, 2020) and RStudio version 1.3.1 (RStudio Team 2020) to assess interobserver reliability using the kappa2 function in the *irr* package (Gamer et al., 2012) and found that Kappa = 0.995. S.M.L. and S.C.M. disagreed on one tooth from one session: where S.M.L. scored Present, S.C.M. scored Z. We reassessed this session and decided to score the tooth Z. After excluding sessions for which we scored all teeth as Z, our sample included 76 bonobo sessions and 16 chimpanzee sessions.

We aggregated raw scores in two ways: first, we used a single score for left and right sides of the mouth; thus, if we scored Present or Absent for a given tooth on one side and Z on the other side, we used the Present or Absent score, respectively; if we scored Present on one side and Absent on the other side, we used the most dentally advanced score (i.e., Present). Second, we used a single score for each session; thus, if we scored Present or Absent for a given tooth in one photograph or video still and Z for another photograph or video still from the same individual on the same day, we used the Present or Absent score, respectively. While previous studies have found considerable and intriguing asymmetry in dental eruption timing both between left and right sides of the mouth as well as between the maxilla and mandible (e.g., Monson & Hlusko, 2018), we opted to collapse the data given sample size limitations.

In our results, we included data for mandibular deciduous teeth from the Kanyawara population of East African chimpanzees, which we estimated from Machanda et al. (2015; figure 2); these Kanyawara datapoints represent the age of the youngest individual for which emergence of the tooth was observed or the age of the youngest individual for which the tooth was observed to be past emergence in cases when emergence was not directly observed. We did not include maxillary data from the Kanyawara chimpanzee population because Machanda et al. (2015) did not report deciduous eruption ages for maxillary teeth. We also included captive chimpanzee deciduous emergence age ranges from Kuykendall et al. (1992). Lastly, we did not consider whether a tooth may have erupted but then was subsequently lost. While this may be unlikely, our criteria for Absent assumes that the tooth had not yet emerged.

The ideal standard for studies of dental eruption timing would be longitudinal observations of tooth emergence from a large sample of subjects conducted systematically at short intervals (i.e., on a daily basis), and over the full duration of development. Or, failing this, sufficient sampling to allow for the calculation of age at emergence for each population using, for example, cumulative distribution functions (see Smith, 1991). However, the current study does not meet these criteria. The sample is small and opportunistic; observations were conducted at irregular and often extended intervals, and some ages are poorly represented for any given tooth type. Nevertheless, these data are still extremely valuable given the dearth of data on deciduous dental eruption in wild apes.

2.4 | Ethics statement

All methods used in the field were noninvasive and were approved by the Institut Congolaise pour la Conservation de la Nature and the Tanzania Wildlife Research Institute. All aspects of the study comply with the ethics policy of The George Washington University Office of Animal Research Policies and Procedures (https://animalresearch.gwu.edu/) and the guidelines for the ethical treatment of nonhuman primates of the Max Planck Institute for Evolutionary Anthropology (https://www.eva.mpg.de/primat/ethical-guidelines.html).

3 | RESULTS

The youngest bonobo and chimpanzee that we scored was 62 days old and 120 days old, respectively. The youngest bonobo that we observed to have deciduous teeth present in our sample was 88 days old. The sequence of maxillary eruption in our bonobo sample, beginning with the earliest to erupt, is as follows: first incisor; second incisor and third premolar; fourth premolar and canine. The sequence of mandibular eruption in our bonobo sample is as follows: first incisor; second incisor and third premolar; fourth premolar; canine. We did not extrapolate an eruption sequence for chimpanzees because the youngest individual in our sample was already 120 days old. Machanda et al. (2015) reported the following eruption sequence in Kanyawara chimpanzees: first incisor, second incisor, third premolar,

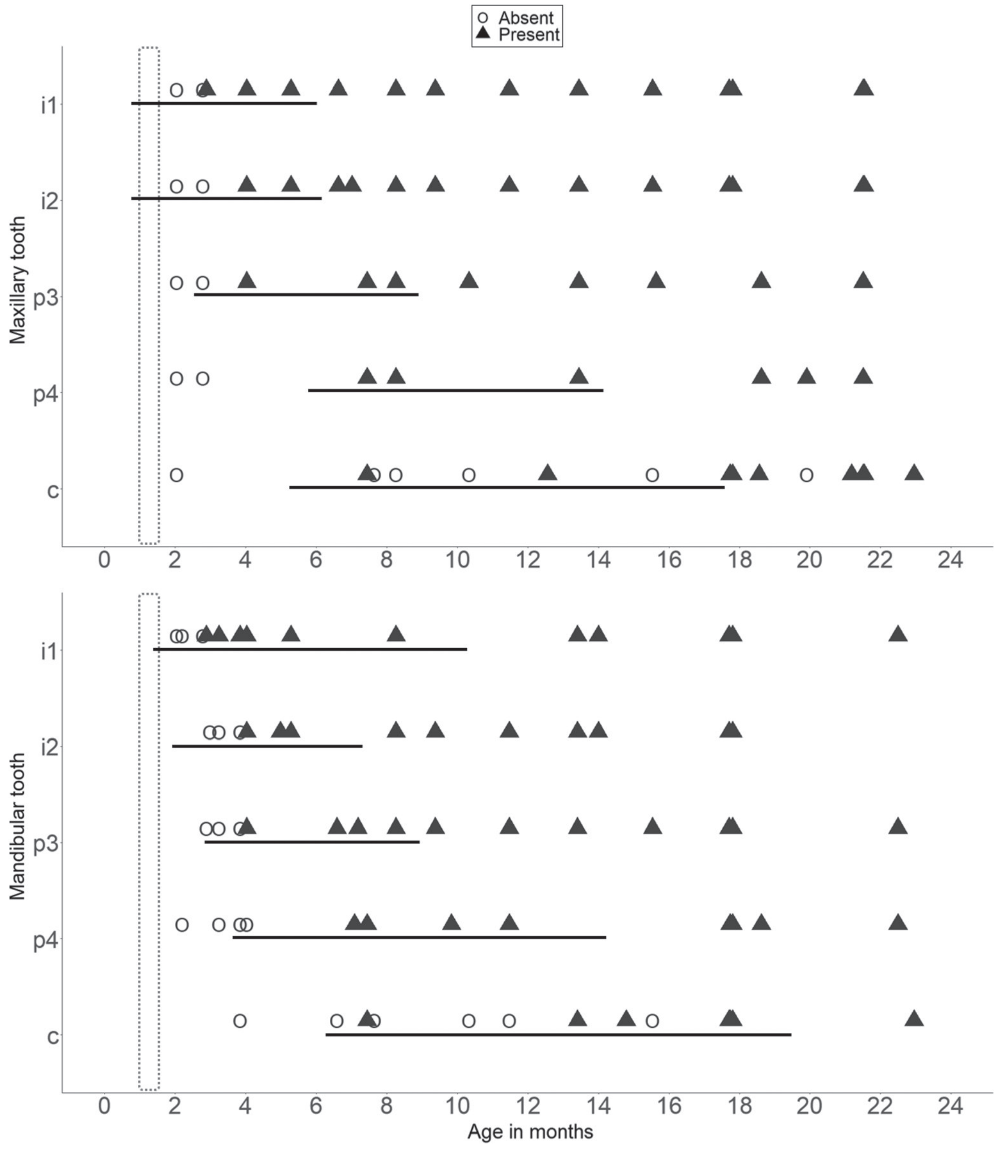

FIGURE 1 Presence/absence of maxillary and mandibular deciduous teeth in LuiKotale bonobos. For each tooth, an open circle represents a session for which we scored the tooth as Absent, and a filled triangle represents a session for which we scored the tooth as Present. Black horizontal bars represent age ranges for tooth emergence in 41–51 captive chimpanzees from Kuykendall et al. (1992; table 2). Dotted vertical bar represents age range for earliest deciduous tooth emergence in four captive bonobos from Neugebauer (1980). In Figures 1 and 2, we utilized criteria to avoid repeated and irrelevant observations for a given individual and tooth: Where we have multiple longitudinal sessions of an individual, we only included the last session for which we scored a given tooth as Absent and the first session for which we scored that tooth as Present. Importantly, due to uneven sampling of individuals, a score of Present does not necessarily indicate that the tooth recently erupted in that individual, as this could also indicate that the individual was not sampled regularly prior to the first time that we scored the tooth as Present in that individual. i1, incisor 1; i2, incisor 2; c, canine; p3, premolar 3; p4, premolar 4

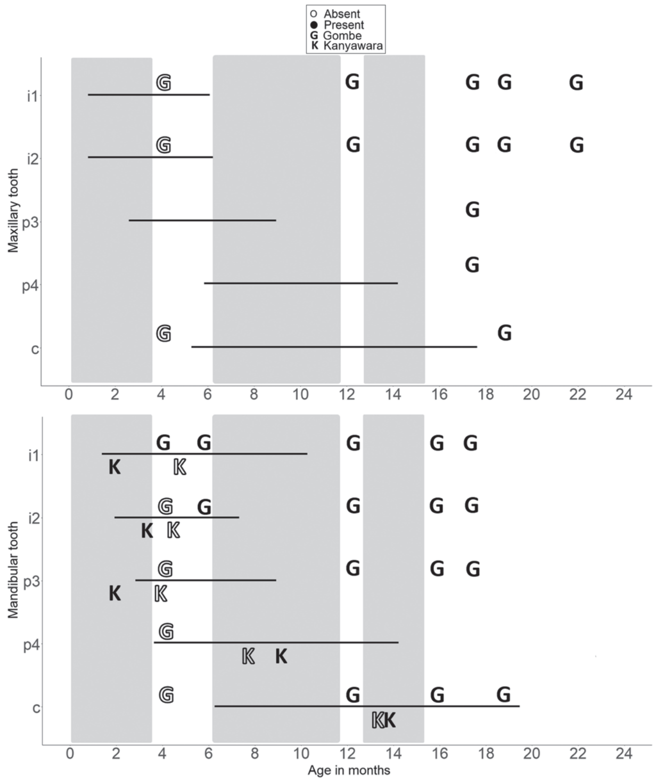

FIGURE 2 Presence/absence of maxillary and mandibular deciduous teeth in Gombe chimpanzees. For each tooth, an open G represents a session for which we scored the tooth as Absent, and a filled G represents a session for which we scored the tooth as Present. Data from Kanyawara are from Machanda et al. (2015; figure 2): A filled K represents age at emergence or youngest age when the tooth was observed to be past emergence in cases when emergence was not directly observed and an open K indicates the oldest age for which the tooth was observed to be Absent. Black horizontal bars represent age ranges for tooth emergence in 41–51 captive chimpanzees from Kuykendall et al. (1992; table 2). Gray shaded areas represent sampling gaps greater than 3 months during which we obtained no dental data from Gombe. i1, incisor 1; i2, incisor 2; c, canine; p3, premolar 3; p4, premolar 4

fourth premolar, and canine. Figures 1 and 2 illustrate aggregated Present/Absent scores by tooth type for maxillary and mandibular teeth in our bonobo and chimpanzee samples, respectively. Table 1 includes age ranges for the oldest age at which a tooth was scored as Absent and the youngest age at which it was scored as Present for each population. Tables S2 and S3 include aggregated raw scores for LuiKotale and Gombe, respectively.

4 | DISCUSSION

This is the first study, to our knowledge, that reports dental eruption timing in living, wild bonobos. As such, this study expands our understanding of great ape life history and provides a benchmark with which to compare to future dental eruption studies on wild great apes. Furthermore, this study contributes to the limited body of dental eruption data from living, wild chimpanzees. Future studies may pair our findings with additional data to further elucidate the temporal relationship between tooth eruption and other life history variables within and between hominoid taxa, which may not be as tightly linked (e.g., Rozzi, 2016) as previous studies have concluded (see Section 1).

Our eruption ages for both bonobos and chimpanzees fall within the range of variation found in a large sample of captive chimpanzees (Kuykendall et al., 1992). However, the earliest deciduous teeth to erupt in the captive chimpanzee sample analyzed by Kuykendall et al. (1992) erupted at 0.07 years (approximately 26 days) and the earliest to erupt in the captive bonobo sample analyzed by Neugebauer (1980) erupted between 28–42 days. Therefore, the earliest ages of eruption in both of these captive samples are earlier than in our wild bonobo sample (88 days) and in the Kanyawara wild chimpanzee sample (approximately 50 days as estimated from Machanda et al. (2015; figure 2)). This suggests that deciduous teeth begin to emerge later in wild (approximately 50–88 days) than in captive (approximately 26–42 days) individuals.

The apparent earlier eruption of deciduous teeth in captive individuals relative to wild individuals may be due to enhanced nutrition

TABLE 1 Deciduous tooth Present/Absent age ranges

		LuiKotale		Gombe	
	Tooth	Oldest age absent (days)	Youngest age present (days)	Oldest age absent (days)	Youngest age present (days)
Maxillary	i1	85	88	120	261
	i2	85	123	120	261
	c	477	227	120	571
	p3	85	123	—	526
	p4	85	227	—	526
Mandibular	i1	85	88	—	120
	i2	117	123	123	175
	c	474	227	261	371
	p3	117	123	120	261
	p4	123	216	120	—

Note: "—" indicates that no score of present or absent was made for the given tooth.

and health in captive contexts that results in accelerated development in captive individuals. However, Smith et al. (2013) showed that first permanent molar eruption ages did not differ between captive and wild chimpanzees. It may be the case that the timing of deciduous tooth eruption is more sensitive to environmental conditions than is the timing of permanent tooth eruption. While it is difficult to explicitly test effects of enhanced nutrition and health on captive individuals, our results warrant caution in basing conclusions off captive great ape deciduous dental eruption studies (but see Behringer et al. (2021) for evidence that captive versus wild context does not influence aspects of physiological ontogeny).

One of the most striking results from our study is the high variation in deciduous canine eruption timing. The youngest bonobo in our sample with a canine present was WAT (male) at 227 days old (Figure 1; Figure S1d), while the oldest bonobo yet to have a canine was PIP (female) at 477 days old. The youngest chimpanzee with a canine present was GOS (female) at 371 days old, but we again acknowledge the large gaps in our sampling interval, particularly for chimpanzees during the early ages of life (Figure 2). The earliest age of mandibular canine eruption in the Kanyawara chimpanzee sample was approximately 440 days (Machanda et al., 2015; figure 2). Importantly, the earliest age of mandibular canine eruption in the captive chimpanzee sample analyzed by Kuykendall et al. (1992) was approximately 186 days, which is considerably earlier than all wild canine eruption ages and further supports the notion that captive individuals exhibit accelerated deciduous dental development relative to wild individuals (see above). High variation in deciduous canine eruption timing is consistent with high variation in permanent canine eruption timing (e.g., Harvati, 2000; Leigh et al., 2005), suggesting that both deciduous and permanent canines are important correlates of within and/or between species variation in infant and adolescent development, respectively. Interestingly, Smith et al. (1994) indicated that the pattern of deciduous canine eruption occurring last in the sequence of deciduous tooth eruption, a pattern that we corroborated, is characteristic of apes and not of other primates. Future studies should explore relationships between variation in deciduous and permanent canine eruption ages and ecological parameters, maternal characteristics, phylogeny, and other aspects of infant development.

Our data also fail to support the hypothesis that bonobos exhibit delayed development compared to chimpanzees (reviewed in Gruber & Clay, 2016), given that bonobo canines erupted earlier than in both the Kanyawara and Gombe chimpanzee populations. While our present results only pertain to deciduous dental development, they are consistent with recent direct comparisons of behavioral (Lee et al., 2020) and physiological (Tkaczynski et al., 2020) development in wild bonobos and chimpanzees, which also failed to detect systematic differences in developmental timing between the two species.

It is important to note that the male bonobo in our sample with the canine present at 227 days old, WAT, had earliest and latest possible birthdates separated by 46 days. As we described in the methods, we calculated the birthdate as the midpoint of this range; thus, the error associated with WAT's birthdate is 23 days. Using the earliest and latest possible birthdates for WAT, his canine would have been present at 204 or 250 days of age, respectively.

Our data indicate that deciduous dental eruption ages for wild individuals fall within the range of variation for captive individuals, but that wild individuals exhibit later eruption. Our data also underscore the high degree of potentially salient interindividual variation in eruption timing found in previous studies. While we could not investigate sources of such variation given sample size constraints, high interindividual variation in deciduous canine eruption timing in particular represents an important subject of continued study as data from more populations become available. Specifically, more systematic observations at shorter observation intervals and over a larger sample of individuals throughout development are needed to generate statistical treatments regarding the relationship between interindividual variation in emergence ages and other variables, such as sex and maternal characteristics. Additionally, in vivo data from West and Central African chimpanzee populations, as well as other bonobo populations, are needed.

ACKNOWLEDGMENTS

We thank the Institut Congolais pour la Conservation de la Nature (ICCN) for granting permission to conduct fieldwork on bonobos in the Salonga National Park buffer zone, the people of Lompole for facilitating research on bonobos in their forest, and Tanzania National Parks, the Tanzania Wildlife Research Institute, and the Tanzanian Commission for Science and Technology for granting us permission to conduct fieldwork on chimpanzees in Gombe National Park. We are extremely grateful to our many local collaborators at the LuiKotale Bonobo Project and the Jane Goodall Institute's Gombe Stream Research Centre, particularly Lambert Booto, Mara Etike, Dr. Deus Mjungu, Madua Musa, Dismas Mwacha, and Sampson Pindu. We thank Dr. Joel Bray, Dr. Ian Gilby, and Dr. Kaitlin Wellens for contributing videos/photographs from which data for the current study were collected, and Zoe Andris, Sarah Fierman, Rosalie Mattiola, and Akhil Vedere for their assistance in screening and extracting still images from video footage. We also thank The George Washington University Primate Behavioral Ecology Lab and Primate Life History Lab for helpful feedback. We thank the following agencies and institutions for their funding support of this work.

CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Sean M. Lee: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing - original draft; writing-review & editing. **L. J. Sutherland:** Data curation; writing-review & editing. **Barbara Fruth:** Conceptualization; data curation; funding acquisition; project administration; resources; supervision; writing-review & editing. **Carson M. Murray:** Conceptualization; data curation; funding acquisition; project administration; resources; supervision; writing-review & editing. **Elizabeth V. Lonsdorf:** Data curation; funding acquisition;

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DATA AVAILABILITY STATEMENT

Data used in this study are available in the supporting information.

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REFERENCES

Behringer, V., Deimel, C., Stevens, J. M. G., Kreyer, M., Lee, S. M., Hohmann, G., Fruth, B., & Heistermann, M. (2021). Cell-mediated immune ontogeny is affected by sex but not environmental context in a long-lived primate species. *Frontiers in Ecology and Evolution*, *9*, 272. https://doi.org/10.3389/fevo.2021.629094

Bolter, D. R., & Zihlman, A. L. (2011). Brief communication: Dental development timing in captive *Pan Paniscus* with comparisons to *Pan Troglodytes*. *American Journal of Physical Anthropology*, *145*(4), 647–652. https://doi.org/10.1002/ajpa.21517

Bromage, T. G., & Christopher Dean, M. (1985). Re-evaluation of the age at death of immature fossil hominids. *Nature*, *317*(6037), 525–527.

Conroy, G. C., & James Mahoney, C. (1991). Mixed longitudinal study of dental emergence in the Chimpanzee, *Pan Troglodytes* (Primates, Pongidae). *American Journal of Physical Anthropology*, *86*(2), 243–254. https://doi.org/10.1002/ajpa.1330860212

Gamer, M., Lemon, J., Fellows, I., and Singh, P. (2012). "Package 'Irr.'" *Various Coefficients of Interrater Reliability and Agreement*.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., & Sutherland, M. R. (2001). Teeth, brains, and primate life histories. *American Journal of Physical Anthropology*, *114*(3), 192–214. https://doi.org/10.1002/1096-8644(200103)114:3<192::AID-AJPA1020>3.0.CO;2-Q

Gruber, T., & Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. *Evolutionary Anthropology: Issues, News, and Reviews*, *25*(5), 239–252. https://doi.org/10.1002/evan.21501

Harvati, K. (2000). Dental eruption sequence among colobine Primates. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *112*(1), 69–85.

Kelley, J., & Schwartz, G. T. (2012). Life-history inference in the early hominins Australopithecus and Paranthropus. *International Journal of Primatology*, *33*(6), 1332–1363. https://doi.org/10.1007/s10764-012-9607-2

Kelley, J., Schwartz, G. T., & Smith, T. M. (2020). Age at first molar emergence in *Pan Troglodytes verus* and variation in the timing of molar emergence among free-living chimpanzees. *Journal of Human Evolution*, *145*, 102823. https://doi.org/10.1016/j.jhevol.2020.102823

Kraemer, H. C., Horvat, J. R., Doering, C., & McGinnis, P. R. (1982). Male chimpanzee development focusing on adolescence: Integration of behavioral with physiological changes. *Primates*, *23*(3), 393–405.

Kuykendall, K. L., James Mahoney, C., & Conroy, G. C. (1992). Probit and survival analysis of tooth emergence ages in a mixed-longitudinal sample of chimpanzees (*Pan Troglodytes*). *American Journal of Physical Anthropology*, *89*(3), 379–399. https://doi.org/10.1002/ajpa.1330890310

Lee, S. M., Murray, C. M., Lonsdorf, E. V., Fruth, B., Stanton, M. A., Nichols, J., & Hohmann, G. (2020). Wild bonobo and chimpanzee females exhibit broadly similar patterns of behavioral maturation but some evidence for divergence. *American Journal of Physical Anthropology*, *171*(1), 100–109. https://doi.org/10.1002/ajpa.23935

Leigh, S. R., Setchell, J. M., & Buchanan, L. S. (2005). Ontogenetic bases of canine dimorphism in anthropoid Primates. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *127*(3), 296–311.

Machanda, Z., Brazeau, N. F., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Wrangham, R., & Smith, T. M. (2015). Dental eruption in east African wild chimpanzees. *Journal of Human Evolution*, *82*, 137–144. https://doi.org/10.1016/j.jhevol.2015.02.010

Mahoney, P. (2019). Root growth and dental eruption in modern human deciduous teeth with preliminary observations on great apes. *Journal of Human Evolution*, *129*(April), 46–53. https://doi.org/10.1016/j.jhevol.2018.12.011

Monson, T. A., & Hlusko, L. J. (2018). Breaking the rules: Phylogeny, not life history, explains dental eruption sequence in primates. *American Journal of Physical Anthropology*, *167*(2), 217–233.

Neugebauer, W. (1980). The status and Management of the Pygmy chimpanzee Panpaniscus in European zoos. *International Zoo Yearbook*, *20*(1), 64–70. https://doi.org/10.1111/j.1748-1090.1980.tb00944.x

Nissen, H. W., & Riesen, A. H. (1964). The eruption of the permanent dentition of chimpanzee. *American Journal of Physical Anthropology*, *22*(3), 285–294. https://doi.org/10.1002/ajpa.1330220315

Pusey, A. E. (1978). The Physical and Social Development of Wild Adolescent Chimpanzees (*Pan Troglodytes* Schweinfurthii). US: ProQuest Information & Learning.

R Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria.

R Studio Team. (2020). RStudio: Integrated development environment for R. Boston, MA.

Robson, S. L., & Wood, B. (2008). Hominin life history: Reconstruction and evolution. *Journal of Anatomy*, *212*(4), 394–425. https://doi.org/10.1111/j.1469-7580.2008.00867.x

Rozzi, F. R. (2016). Diversity in tooth eruption and life history in humans: Illustration from a Pygmy population. *Scientific Reports*, *6*(1), 1–10.

Smith, B. H. (1989). Dental development as a measure of life history in primates. *Evolution*, *43*(3), 683–688.

Smith, B. H. (1991). *Standards of human tooth formation and dental age assessment*. Wiley-Liss Inc.

Smith, B. H. (1992). Life history and the evolution of human maturation. *Evolutionary Anthropology: Issues, News, and Reviews*, *1*(4), 134–142.

Smith, B. H., & Boesch, C. (2011). Mortality and the magnitude of the 'wild effect' in chimpanzee tooth emergence. *Journal of Human Evolution*, *60*(1), 34–46. https://doi.org/10.1016/j.jhevol.2010.08.006

Smith, B. H., Crummett, T. L., & Brandt, K. L. (1994). Ages of eruption of primate teeth: A compendium for aging individuals and comparing life histories. *American Journal of Physical Anthropology*, *37*(S19), 177–231. https://doi.org/10.1002/ajpa.1330370608

Smith, T. M., Machanda, Z., Bernard, A. B., Donovan, R. M., Papakyrikos, A. M., Muller, M. N., & Wrangham, R. (2013). First molar eruption, weaning, and life history in living wild chimpanzees. *Proceedings of the National Academy of Sciences*, *110*(8), 2787–2791. https://doi.org/10.1073/pnas.1218746110

Smith, T. D., Muchlinski, M. N., Jankord, K. D., Progar, A. J., Bonar, C. J., Evans, S., Williams, L., Vinyard, C. J., & Deleon, V. B. (2015). Dental maturation, eruption, and gingival emergence in the upper jaw of newborn primates. *The Anatomical Record*, *298*(12), 2098–2131.

Tkaczynski, P. J., Behringer, V., Ackermann, C. Y., Fedurek, P., Fruth, B., Girard-Buttoz, C., Hobaiter, C., Lee, S. M., Löhrich, T., Preis, A., Samuni, L., Zommers, Z., Zuberbühler, K., Deschner, T., Wittig, R. M., Hohmannan, G., & Crockford, C. (2020). Patterns of urinary cortisol levels during ontogeny appear population specific rather than species specific in wild chimpanzees and bonobos. *Journal of Human Evolution*, *147*, 102869.

Zihlman, A. L., Bolter, D. R., & Boesch, C. (2004). Wild chimpanzee dentition and its implications for assessing life history in immature Hominin fossils. *Proceedings of the National Academy of Sciences*, *101*(29), 10541–43. https://doi.org/10.1073/pnas.0402635101

Zihlman, A. L., Bolter, D. R., & Boesch, C. (2007). Skeletal and dental growth and development in chimpanzees of the Taï National Park, Côte D'ivoire. *Journal of Zoology*, *273*(1), 63–73. https://doi.org/10.1111/j.1469-7998.2007.00301.x