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RESEARCH ARTICLE

Early Brain Growth Cessation in Wild Virunga Mountain Gorillas (*Gorilla beringei beringei*)

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Understanding the life history correlates of ontogenetic differences in hominoid brain growth requires information from multiple species. At present, however, data on how brain size changes over the course of development are only available from chimpanzees and modern humans. In this study, we examined brain growth in wild Virunga mountain gorillas using data derived from necropsy reports ($N = 34$) and endocranial volume (EV) measurements ($N = 86$). The youngest individual in our sample was a 10-day-old neonatal male with a brain mass of 208 g, representing 42% of the adult male average. Our results demonstrate that Virunga mountain gorillas reach maximum adult-like brain mass by 3–4 years of age; adult-sized EV is reached by the time the first permanent molars emerge. This is in contrast to the pattern observed in chimpanzees, which despite their smaller absolute brain size, reportedly attain adult brain mass approximately 1 year later than Virunga mountain gorillas. Our findings demonstrate that brain growth is completed early in Virunga mountain gorillas compared to other great apes studied thus far, in a manner that appears to be linked with other life history characteristics of this population. Am. J. Primatol. 75:450–463, 2013.

Key words: brain growth; mountain gorillas; life history

INTRODUCTION

Questions about the ontogeny of brain size have figured prominently in discussions concerning primate life history evolution and cognitive development [Barrickman et al., 2008; Barton & Capellini, 2011; Bromage et al., 2012; Leigh, 2004; Martin, 1983; Sacher & Staffeldt, 1974]. Because adult brain mass in modern humans is approximately three times larger than expected for a primate of comparable body size [Sherwood et al., 2008], considerable attention has been paid to understanding how such extraordinary encephalization is achieved during ontogeny. Early comparative analyses revealed a positive relationship among brain size and many life history variables, leading to the notion that brain size is inextricably linked to the pace of an organism's schedule of growth and reproduction [Harvey et al., 1987; Sacher & Staffeldt, 1974]. Consistent with this idea, it has been proposed that an extended juvenile period might allow more time to grow a larger brain,

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and may also provide a longer window for cognitive development [Kaplan et al., 2000; reviewed by Robson & Wood, 2008]. However, based on recent studies, brain growth trajectories for modern humans and chimpanzees do not support this expectation. Instead, modern humans achieve significantly larger adult brain size primarily as a consequence of faster growth during the first 18 months of postnatal development. Modern humans attain adult brain mass only slightly later than chimpanzees (90–100% of adult brain mass at 5–7 and 4–5 years, respectively), despite their significantly larger adult brain size and later age at sexual maturity [Coqueugniot & Hublin, 2012; Leigh, 2004; Martin, 1983; Neubauer et al., 2012; Robson & Wood, 2008]. This difference is all the more interesting given that modern humans attain a smaller proportion of adult brain size at birth compared to chimpanzees (27% versus 36%, respectively) [Robson & Wood, 2008]. However, available comparative data against which to evaluate the distinctiveness of human brain growth among hominoids are based entirely on one species of chimpanzee (*Pan troglodytes*).

Primates show considerable diversity in brain growth patterns [Barton & Capellini, 2011; Leigh, 2004; Martin, 1983; Phillips & Sherwood, 2008; Sacher & Staffeldt, 1974]. A relatively large adult brain size can be achieved through a prolonged period of postnatal brain growth, a faster rate of brain growth, or by allocating a greater proportion of brain growth to the prenatal period. Leigh [2004] suggested that the manner in which primates alter these components of brain growth underlies important differences in life history and maternal metabolic strategies. Compared to other primates, modern humans and chimpanzees allocate a large proportion of brain growth to the postnatal period [Leigh, 2004]. Further, humans also incur high energetic costs associated with rapid early postnatal brain growth and processes of synaptogenesis [Chugani & Phelps, 1986; Huttenlocher & Dabholkar, 1997]. However, very little is known about patterns of brain growth among other great apes, and if they vary, what factors might account for these differences.

Virunga mountain gorillas are critical to our understanding of diversity in patterns of brain growth and life history among hominoids because they represent an ecological extreme among the great apes. Mountain gorillas (*Gorilla beringei beringei*) are a subspecies of eastern gorilla, found in two geographically isolated populations, one in the Virunga Volcanoes region of Rwanda, Democratic Republic of Congo, and Uganda, and the other in Bwindi Impenetrable National Park of southwestern Uganda [Groves, 2001]. The high-altitude Afro-montane forests inhabited by mountain gorillas on the slopes of the Virunga Volcanoes range from 2,300 to 4,507 m in elevation, the highest elevational range of any great ape [Kalpers et al., 2003; Stewart et al., 2001]. Also, as fruit is rare in these higher altitude vegetation zones, Virunga mountain gorilla diets rely heavily on the leaves, stems, pith, and shoots of terrestrial herbaceous vegetation, which is abundant year-round and densely distributed [Fossey & Harcourt, 1977; McNeilage, 2001; Watts, 1984, 1996]. Their diets show little intraannual variability, except for their use of seasonally abundant bamboo shoots [Watts, 1998].

The unique dietary ecology of mountain gorillas is proposed to have an influence on their social relationships and grouping patterns, and they differ from other great apes in many important aspects of their life histories [Harcourt & Stewart, 2007; Robbins, 2007; Sterck et al., 1997; Watts & Pusey, 1993]. Despite their considerably larger adult body size, Virunga mountain gorillas from the Karisoke study area wean their infants at younger ages, have younger ages at first birth, and shorter interbirth intervals than do wild chimpanzees [Watts & Pusey, 1993]. Furthermore, long-term data accumulating from other wild study populations suggest there may also be marked differences in life history among gorilla taxa. For instance, other eastern gorilla populations and western lowland gorillas (*Gorilla gorilla gorilla*) show later ages at weaning, later ages at first birth as well as lower fertility, in accordance with an increased dietary consumption of fruit [Breuer et al., 2009; Robbins et al., 2004, 2009; Yamagiwa & Kahekwa, 2001].

Relatively little is known about the physical ontogeny of gorillas, which has been best characterized for body mass in captive animals of known chronological age. Compared to other African great apes, captive western gorillas achieve their larger adult size primarily as a consequence of higher growth rates [Leigh, 1994; Leigh & Shea, 1995, 1996]. Further, female western gorillas achieve almost twice the adult body mass of female chimpanzees, yet they stop growing nearly 2 years earlier [Leigh & Shea, 1996].

The accelerated life history strategies of mountain gorillas compared to other great apes has been explained within the context of the metabolic risk aversion hypothesis, which posits a relationship between elevated feeding competition associated with more frugivorous diets and selection for low growth rates [Breuer et al., 2009; Janson & van Schaik, 1993; Leigh, 1994, 1995; Leigh & Shea, 1995, 1996]. Examination of brain growth in mountain gorillas, the least frugivorous of the great apes, provides an important opportunity to assess life history diversity within the ecological spectrum of hominoids. If brain size ontogeny bears a relationship to life history and ecology, as proposed, we expect mountain gorillas to show accelerated brain size development, as they do for body size and reproductive development, compared to humans and chimpanzees.

Prior studies comparing neuroanatomical variation among great apes have included only adults, and have rarely included mountain gorillas [Aldridge, 2011; Barger et al., 2007; Herculano-Houzel & Kaas, 2011; Hopkins et al., 2009; Rilling & Insel, 1999; Rilling et al., 2012; Sherwood & Hof, 2007; Stimpson et al., 2011]. Previous research based on small sample sizes of adults has examined external brain morphology, fissural pattern, brain stem anatomy, and volumes of major structures in mountain gorilla brains [Hosokawa & Kamiya, 1963a, 1963b; Hosokawa et al., 1965; Sherwood et al., 2004]. Further, most compilations of endocranial volume (EV) data in great apes only report summary statistics for gorillas, without specifying taxonomy or geographic locality of origin [e.g., Holloway, 1996; Tobias, 1971]. Consequently, data on EV of mountain gorillas has only occasionally been reported separately [Isler et al., 2008]. In contrast, more precise data regarding variation in brain size (or EV) as it relates to ontogeny, subspecies differences, and sexual dimorphism are available for other great ape species [Durrleman et al., 2012; Leigh, 2004; Neubauer et al., 2012; Taylor & van Schaik, 2007]. Information regarding the ontogeny of gorilla brains is almost entirely absent, aside from data on neonatal brain mass in a small number of captive western lowland gorillas [DeSilva & Lesnik, 2008; Martin, 1983; Sacher & Staffeldt, 1974].

Here, we present new data on EV and brain mass growth from the largest sample of mountain gorillas ever examined. Our results have implications for understanding variation in brain size ontogeny in humans and great apes, and its relationship to differences in ecology and life history.

METHODS

This research relied exclusively on data collected from postmortem specimens of wild gorillas that accumulated as a result of natural deaths, and museum specimens; no living animals were used in this study. The acquisition of necropsy data on brain mass and measurement of skeletal samples are exempted from the requirement of approval by the Institutional Animal Care and Use Committee. The research presented here is in accordance with the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates, and adhered to the legal requirements of Rwanda.

Sample

We examined measures of brain mass and EV in mountain gorillas (*G. beringei beringei*) from the Virunga Volcanoes of East-Central Africa, which includes protected area habitat that straddles the border between neighboring parts of Rwanda (Volcanoes National Park), Democratic Republic of Congo (Parc National des Virungas), and Uganda (Mgahinga Gorilla National Park). Individuals included in the current study are derived from two main sources, as explained below.

(1) *Recent Mountain Gorillas from Rwanda*. Brain mass and EV data in this subset of our study sample are derived from gorillas that lived in Volcanoes National Park in Rwanda. Many of these individuals were from habituated groups monitored on a daily basis by the Rwanda national parks authority (now the Rwanda Development Board, RDB) or Dian Fossey Gorilla Fund International's (DFGFI) Karisoke Research Center staff, for tourism and research, respectively [Fossey, 1983; Robbins et al., 2011]. The Mountain Gorilla Veterinary Project (MGVP) monitors the health of habituated gorillas [Cranfield, 2007]. When monitoring patrols encounter the remains of deceased gorillas in the forest, postmortem veterinary exams (i.e., necropsies) are performed by the MGVP where preservation conditions permit. In such cases, individual identity is determined from unique identifiers (e.g., nose prints) and verified based on individual disappearances from monitored social groups. In such cases where a body is found at an advanced stage of decomposition, genetic sampling is undertaken to confirm suspected individual identities. Brain mass data collected at necropsy from a total of 34 individuals have been made available for the current study (Table I).

As it has been common protocol to bury the remains of deceased gorillas after necropsy, the Mountain Gorilla Skeletal Project (MGSP) was initiated in 2008 as a multidisciplinary and collaborative effort to assist RDB in the location, systematic recovery, and preservation of mountain gorilla skeletal remains in Rwanda [McFarlin et al., 2009]. The skeletal collection currently comprises 103 individuals from Volcanoes National Park, many of which represent individually identified gorillas from habituated groups monitored by RDB and Karisoke. Of these, 63 individuals (24 males, 27 females, 12 of unknown sex) preserve cranial anatomy enabling calculation of EV, and are included in this study.

Among the recent mountain gorillas from Rwanda included in this study, many were individually identified gorillas derived from habituated social groups that are monitored daily in Volcanoes National Park. However, the precision of age at death determinations for these individuals varies according to their observation history. This sample also includes gorillas of unconfirmed identity and/or age at death. We therefore provide further clarification on age at death determinations used in our analyses below.

Gorillas of known or approximated age at death (*Table* I). Because habituated social groups are

TABLE I. Individual Data

Name	Age (years)	Sex	Brain mass (g)
Subset A: Individuals of known chronological age			
Agaciro	1.63	Male	501
Agatako	0.50	Male	456
Ahzaza's infant	0.56	Female	339
Akarusho	3.36	Male	439
Arusha	6.08	Male	521[a]
Ginseng	31.15	Female	431
Gukunda's infant	0.10	Male	300
Icyi	2.45	Female	442
Ihumure	3.71	Male	500
Intwali	24.26	Female	479
Iradua	1.92	Female	493
Mahane's infant	0.45	Female	360
Mbele's infant	1.33	Female	390
Mpanga	10.69	Female	444[a]
Mpore	3.83	Female	404
Mugeni's infant	0.73	Female	230
Mutesi	1.67	Female	388
Ndatwa	14.94	Male	460[a]
Ngwino	3.62	Female	388
Ntobo	19.79	Female	495
Nyarusizi	12.71	Male	519[a]
Nzeli's infant	0.14	Male	353
Safari's infant	0.03	Male	208
Sagamba	1.20	Male	390
Shinda	31.74	Male	538
Shyirambere	2.93	Male	392
Tayna	8.61	Female	450
Tayna's infant	0.25	Female	356
Titus	35.05	Male	500
Turahirwa	1.06	Female	409
Umugisha	16.94	Female	433
Umurage	2.41	Female	453[a]
Umurava	21.14	Male	514[a]
Subset B: Individuals of estimated chronological age			
Beetsme[b]	34	Male	459[a]
Cyiza[c]	42	Female	500
Kubyina[d]	30	Female	444[a]
Kuryama[e]	24.8	Male	525[a]
Kwiruka[d]	34	Female	492
Nyakarima[f]	33	Male	466[a]
Pandora[c]	37	Female	494[a]
Puck[g]	38.3	Female	400
Sabana[f]	16	Female	455
Sabinyo infant[f]	2	Female	433
Tuck[g]	38.3	Female	500
Walanza[c]	37	Female	414

Note: Subset A includes individuals for whom birth and death dates are known to the exact day or week (± 4 days; Williamson & Gerard-Steklis, 2001 for Karisoke monitored individuals). Subset B includes individuals with estimated birth dates or death dates (i.e., corresponding to birth errors 1–6 for Karisoke-monitored individuals; Williamson & Gerard-Steklis, 2001). Where age error exceeds ±6 months, estimated chronological age at death is reported to the nearest year.

[a]Brain mass estimated from endocranial volume by least squares regression.

[b]Estimated date of birth (±2 years; birth error 5 for Karisoke monitored individual, Williamson & Gerard-Steklis, 2001).

[c]Estimated date of birth (±4 years; birth error 6 for Karisoke monitored individual, Williamson & Gerard-Steklis, 2001).

[d]Estimated date of birth (±1.5 years; birth error 4 for Karisoke monitored individual, Williamson & Gerard-Steklis, 2001).

[e]Estimated date of death, based on date last observed.

[f]Estimated date of birth.

[g]Estimated date of birth (±15 days; birth error 1 for Karisoke monitored individual, Williamson & Gerard-Steklis, 2001).

visited daily in Volcanoes National Park, individuals born into or dying out of groups under active observation are associated with birth and death dates known to the exact day or week (±4 days for Karisoke monitored groups) [Williamson & Gerard-Steklis, 2001]. All infants, juveniles, and many adults included in this subset of our sample are associated with precisely determined ages at death [age range from 10 days (0.03 years) to 35 years 20 days (35.05 years)], with the exception of Sabyinyo infant for whom age at death is approximated. Eleven adults are of confirmed identity, but their birth or death dates are approximated (errors ranging from ±15 days to ±4 years) [Williamson & Gerard-Steklis, 2001]. These individuals typically (a) immigrated as unhabituated individuals into a social group under study, (b) were first observed as an older infant, juvenile or adult, or (c) disappeared from a study group and their body later found at an advanced stage of decomposition (as in the case of Kuryama; Table I). In the latter case, date last observed is used as the estimated date of death. Adults of approximated ages at death range from 16 to 42 years of age.

Gorillas for whom individual identity and/or age at death is not currently known (*summarized in Table* II). EV data were collected from 35 gorillas comprising unhabituated individuals of unknown age, and other individuals who may be derived from habituated groups but whose identities have yet to be confirmed. Among the latter, these skeletal specimens represent individuals that died before the MGSP began, and for whom contextual information (namely, burial location) was lost over time prior to initiation of the project. While probable identities for these individuals have been determined, genetic and histologic analyses are underway to provide positive identifications. These individuals are considered "unknown" in the current study; they were only used for analyses of EV in relation to dental emergence stage, as explained below.

(2) *USNM skeletal specimens*. EV data were collected from 23 mountain gorillas (11 males, 10 females, 2 unknown) curated at the Smithsonian

TABLE II. Endocranial Volumes of Mountain Gorillas by Dental Emergence Stage

Dental stage		*N*	Mean (cm^3)	SD	Age class composition, by sex
1	Combined sexes	**2**	**409**	**48**	MGSP (female, $n = 0$; male, $n = 1$; unknown, $n = 1$) USNM (female, $n = 0$; male, $n = 0$; unknown, $n = 0$)
2	Combined sexes	**13**	**446**	**50**	MGSP (female, $n = 3$; male, $n = 3$; unknown, $n = 6$) USNM (female, $n = 0$; male, $n = 1$; unknown, $n = 0$)
	MGSP females	3	425	47	
	MGSP males	3	466	32	
3	Combined sexes	**9**	**470**	**52**	MGSP (female, $n = 3$; male, $n = 4$; unknown, $n = 2$) USNM (female, $n = 0$; male, $n = 0$; unknown, $n = 0$)
	MGSP females	3	443	24	
	MGSP males	4	512	51	
4	Combined sexes	**3**	**434**	**10**	MGSP (female, $n = 0$; male, $n = 0$; unknown, $n = 2$) USNM (female, $n = 1$; male, $n = 0$; unknown, $n = 0$)
5	Combined sexes	**59**	**493**	**50**	MGSP (female, $n = 22$; male, $n = 15$; unknown, $n = 1$) USNM (female, $n = 9$; male, $n = 10$; unknown, $n = 2$)
	MGSP females	21	476	25	
	MGSP males	16	547	44	
	USNM females	9	431	23	
	USNM males	10	499	27	

Note: Combined sex summary statistics include specimens of unknown sex. Boldface indicates the value for combined sexes from the total sample at each dental stage.

Institution's National Museum of Natural History (USNM). A majority of these specimens were collected by Dian Fossey and colleagues during the late 1960s and 1970s, although three were collected prior to 1950.

Data Collection

Brain masses collected at necropsy

Brain mass data collected by MGVP at necropsy were available for 34 individuals examined here. To prevent distortion of brain mass data resulting from the effects of tissue autolysis, only brains collected within 48 hr of death were used in the current study. In one case (Sabyinyo infant), postmortem interval was estimated at 48–72 hr; however, this brain showed no obvious signs of autolysis and therefore was included. Not all individuals for whom we were able to obtain EVs in the study are also represented by brain masses. However, all individuals with brain masses are associated with known chronological ages at death, as explained above.

In order to increase the sample of individuals with known chronological age at death in our analyses, a prediction equation was generated using least squares regression for cases in which both EV and brain mass were available ($N = 15$; age range = 6 months to 42 years; 11 females, 4 males). With this equation [$y = 0.715x + 116.1$, $r^2 = 0.420$, $P = 0.02$ (where $x = \text{EV}$)], EV was converted to brain mass in the 11 cases for which only EV was available with a known chronological age at death.

Endocranial volume

EV measurements were collected from a total of 86 mountain gorillas, using two methods. In MGSP crania ($n = 63$), EV was measured by depositing sorghum seeds or glass beads into the foramen magnum, tapping the skull to settle and fill all spaces, and then transferring the seeds or beads to a graduated cylinder for measurement. For crania of older infants in which the sutures were unfused, we used masking tape to hold together the separate cranial bones in close apposition. In USNM crania ($n = 23$), EV was measured from CT scans, using MRIcro software's 3D sphere region of interest tool to measure a "virtual" cranial capacity. CT scanning was performed using a SIEMENS Somatom Emotion CT scanner (Siemens Medical, Malvern, PA) (110 kV, 70 mA, 1-mm slice thickness, 0.5-mm reconstruction increment, H90 moderately sharp kernel).

To determine the comparability of data from these two EV measurement techniques, EV was measured using both methods described above for five USNM crania (using glass beads). The values obtained via measurement of virtual cranial capacity varied from those obtained by physical measurement by no more than 2.6%, with no systematic bias in the direction of differences in the EV between techniques. Interobserver consistency in the measurement of EV in the MGSP collection based on seed filling was determined by measuring a subsample of six crania. The intraclass correlation coefficient between observers was 0.99 ($P < 0.001$) and on average the measurements differed from each other by only 1.3%.

Dental emergence status

In the analysis of EV, our sample included individuals of unconfirmed identity and age at death. We therefore used dental development status to group

individuals into five age classes defined on the basis of alveolar emergence [adapted from Shea, 1981, 1982]. Stage 1 includes infants with partial deciduous dentitions, some deciduous teeth having not yet emerged beyond the alveolar margin. Stage 2 includes infants with alveolar emergence of all deciduous teeth. Stage 3 includes juveniles with alveolar emergence of one or more first permanent molars. Stage 4 includes juveniles with alveolar emergence of one or more second permanent molars. Stage 5 includes individuals with alveolar emergence of one or more third permanent molars. While it is recognized that molar root formation continues after emergence, all individuals in Stage 5 were considered adults for the purposes of the current study, given the difficulty of observing root growth from intact skeletal specimens in the field. We followed Shea's dental aging scheme to facilitate future comparative analyses, with the following major modification. Given small sample sizes within each age class and our observation that older age classes were not characterized by significant contrasts in brain size, we chose to lump all individuals with emergent, partially erupted and fully erupted M3s together into Stage 5, whereas Shea [1981, 1982] recognized two additional stages (Shea's dental Stages 6 and 7) on the basis of advanced eruption of the third permanent molar and canine, fusion of the basilar suture, and tooth wear. Finally, we also note that age classes based on dental development may not correspond to age classes based on behavioral or reproductive criteria [e.g., Robbins et al., 2009; Watts & Pusey, 1993].

The sample utilized here was accumulated primarily through natural deaths, with rare exceptions associated with poaching and crop-raiding incidents (namely, in the USNM collection). This places obvious limitations on the representation of different age and sex classes in our study.

Data Analysis

Brain mass and EVs were treated separately to avoid replicates in the data set, given the possibility that some individual data points might be associated with as-of-yet unidentified skeletons (and thus, EV data points) in the MGSP collection.

Brain mass compared to chronological age

Brain mass was analyzed as a function of chronological age, with male and female growth trends determined separately. Piecewise quadratic regression [Leigh, 1994] was used because it is most appropriate in the case of gaps in the data across the age distribution. The break point in this analysis was set at age 10 years. We calculated the arithmetic velocity of brain growth by dividing the difference in successive brain masses on the growth curve by successive ages.

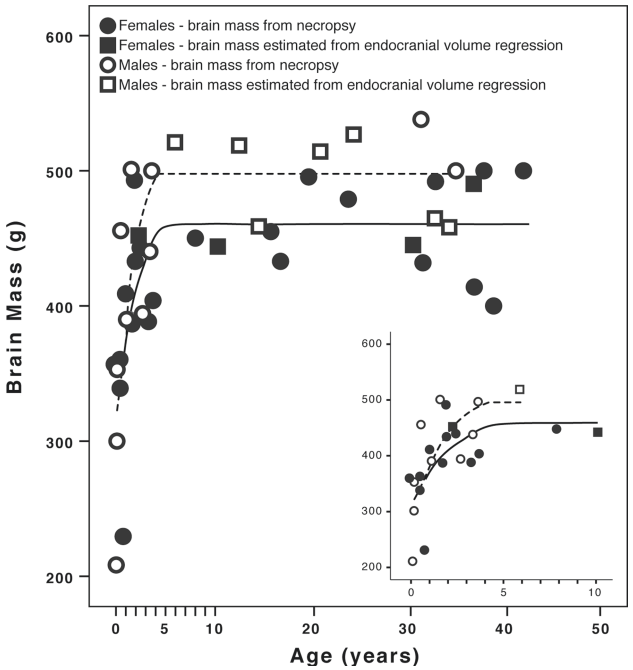

Fig. 1. Brain mass as a function of age. Separate piecewise quadratic regression fits were calculated for males and females. Circles indicate data for brain mass collected at necropsy. Squares indicate brain masses calculated from the prediction equation based on endocranial volume as described in the text. The inset graph shows the same data with a focus on the first 10 years to more clearly illustrate early growth.

Proportional brain mass

Following Coqueugniot and Hublin [2012], proportional brain masses (PBM) were calculated for infants and juveniles by dividing individual brain masses by the average adult value for the corresponding sex of the individual. PBM values reflect the percentage of sex-specific average adult brain mass obtained by immature individuals. Average adult brain mass was calculated separately for males and females of 10 years of age and older, by which time one or more of the M3s has emerged in this sample. A quadratic regression was used to estimate the age at which males and females reach 90% of PBM.

EV comparisons across dental age classes

Because of small sample sizes at early ontogenetic stages, nonparametric Kruskal–Wallis tests and pairwise Mann–Whitney tests were used to assess differences in EV across dental age classes.

RESULTS

Brain Mass Compared to Chronological Age

Average adult brain mass for females was 460 g (SD = 35.1, $N = 13$) and for males it was 498 g (SD = 31.6, $N = 8$). Sex differences in adult brain mass were statistically significant (Mann–Whitney $U = 19$, $P = 0.02$; M/F = 1.082). In both sexes, there was a rapid

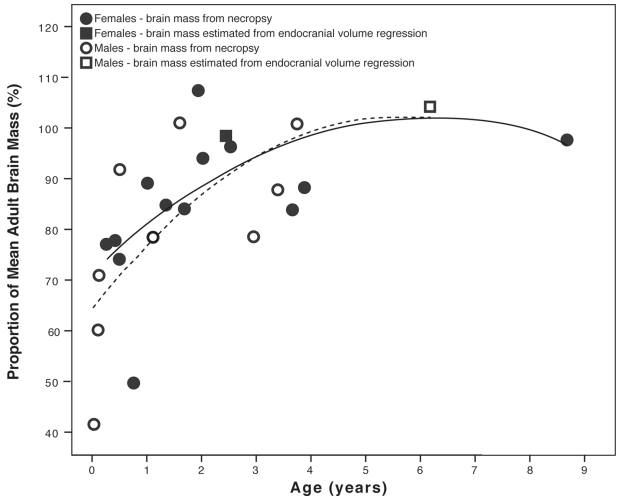

Fig. 2. Proportion of mean adult brain mass in infants and juveniles as a function of age. Circles indicate data for brain mass collected at necropsy. Squares indicate brain masses calculated from the prediction equation based on endocranial volume as described in the text. Lines indicate quadratic regressions calculated for males and females.

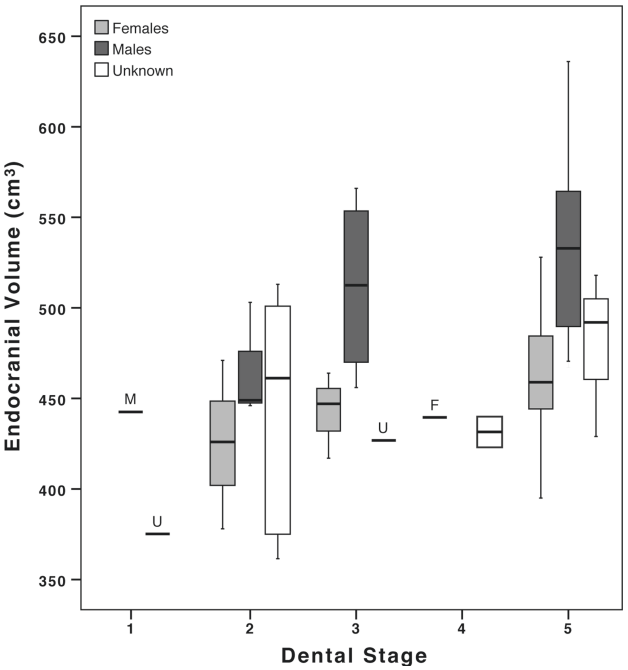

Fig. 3. Boxplots of endocranial volumes by dental emergence stage. The boxes show means and interquartiles; whiskers show ranges. M, male; F, female; U, unknown sex.

increase in brain mass from birth, with the velocity of growth declining by approximately one and a half years of age (Fig. 1). In males, where our sample includes more data from neonates, the growth velocity was 13.7 g/month in the first 6 months, and then declined to a rate of 9.5 g/month by the end of the first year. In females, the growth velocity was 7.5 g/month at 1 year of age. Piecewise regressions provided estimates of age at cessation of brain growth, showing that both males and females have completed brain growth between 3 and 4 years of age. As one infant in our analysis was associated with an estimated age at death (Sabyinyo infant), we also recalculated the piecewise regression fit with this individual removed. Removal of this individual from the data set did not alter our results.

Proportional Brain Mass

The proportion of adult brain mass attained in infants and juveniles further supports the conclusion that wild mountain gorillas reach adult brain size early in development. The youngest individual in this sample (age 10 days) is a male with a brain mass of 208 g, which is 42% of the average adult male brain size. Notably, juveniles reach 90% PBM by approximately 28 months of age based on a quadratic fit to the PBM data (Fig. 2).

EV Comparisons by Dental Emergence Stage

Means and standard deviations for EV by age class are presented in Table II, and boxplots are shown in Figure 3. Differences in EV across dental emergence stages were significant (Kruskal–Wallis $\chi^2 = 16.17$, $P = 0.003$). Significant pairwise differences in EV were identified between dental Stages 1 and 5 (Stage 5 > Stage 1, Mann–Whitney $U = 6.0$, $P = 0.03$), Stages 2 and 5 (Stage 5 > Stage 2, Mann–Whitney $U = 208.5$, $P = 0.01$), and Stages 4 and 5 (Stage 5 > Stage 4, Mann–Whitney $U = 13.0$, $P = 0.01$). All other contrasts between dental stage pairs were nonsignificant. We interpret the significant contrast between Stages 4 and 5 to be an artifact of small sample size; the mean EV of Stage 4 ($n =$ 1 female, two unknown sex) was smaller than Stage 3 (Fig. 3). Thus, these data suggest that adult brain size is obtained by dental Stage 3, which corresponds to alveolar emergence of the first permanent molar.

Adult males exhibited significantly larger EVs than adult females (Mann–Whitney $U = 89.0$, $P <$ 0.0001). Although males had larger EVs than females at dental Stages 2 and 3 (Fig. 3), these differences were not statistically significant (Stage 2: Mann–Whitney $U = 2.0$, $P = 0.28$; Stage 3: Mann–Whitney $U = 1.0$, $P = 0.08$). Small sample sizes precluded similar comparisons between males and females at dental Stages 1 and 4. The degree of sexual dimorphism in EV of mountain gorillas is very close to that observed in wild western lowland gorillas. In our sample, the mean EV of adult females is 88% that of adult males. Similarly, from the data reported in Isler et al. [2008], female western lowland gorillas have EVs that are 87% of the male values (19 females, 36 males).

Temporal Trends in EV

In the main analysis of EV across dental eruption stages, all specimens from the MGSP and USNM samples were pooled together. However, when they were considered separately, statistically significant differences were observed among adults (USNM < MGSP; Mann–Whitney $U = 212.5$, $P = 0.008$). As a subset of the MGSP sample is comprised of individuals of unknown collection date, this contrast remains significant when restricted only to adult USNM samples collected between 1968 and 1983 ($n = 9$ males, 9 females, 2 unknown sex), and MGSP samples collected between 1997 and 2012 ($n = 14$ males, 14 females; Fig. 4). USNM individuals collected prior to 1983 have significantly smaller EVs than those of the MGSP, a majority of which postdate 1997 (Mann–Whitney $U = 426.5$, $P = 0.002$).

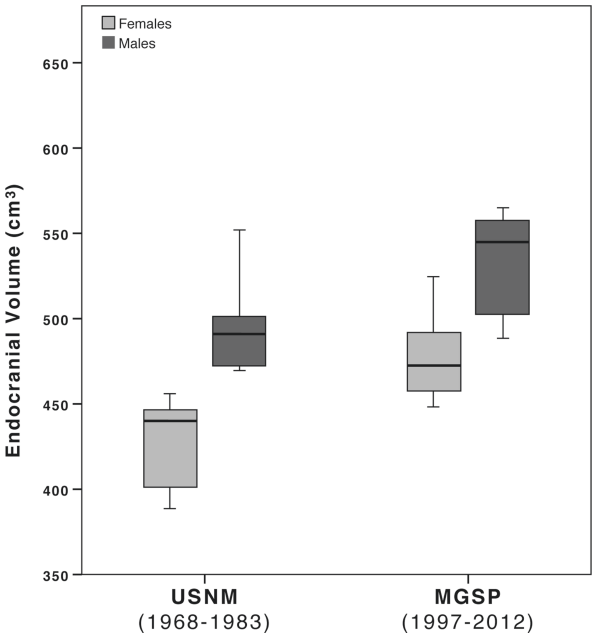

Fig. 4. Differences in adult endocranial volume between USNM individuals (collected between 1968 and 1983; $n = 9$ males, 9 females, 2 unknown sex) and MGSP individuals (collected between 1997 and 2012; $n = 14$ males, 14 females). The boxes show means and interquartiles; whiskers show ranges.

DISCUSSION

Significant postnatal changes in brain size extending through the duration of infancy have been observed in several primate species [Leigh, 2004], including chimpanzees [Herndon et al., 1999; Neubauer et al., 2012] and bonobos [Durrleman et al., 2012]; in humans, brain growth continues through early childhood [Coqueugniot & Hublin, 2012]. In all hominoid species studied, the period of postnatal brain size growth encompasses several years. For instance, Neubauer et al. [2012] report that adult EV is achieved around 5 years of age in wild chimpanzees from the Taï Forest. For modern humans, Coqueugniot and Hublin [2012] found that EV reaches its peak at approximately 7 years of age.

Our results provide the first evidence of postnatal brain growth patterns in any gorilla species. We found that Virunga mountain gorillas cease brain growth between 3 and 4 years of age, thus condensing postnatal brain growth into a shorter period than has been reported for either chimpanzees or humans. Despite having an adult brain size that is roughly 25% larger on average compared to chimpanzees (Table IV), Virunga mountain gorillas reach their adult brain size approximately 1 year earlier. The single neonate in our sample, a 10-day-old male, had a brain mass of 208 g, or 42% of the adult mean. This is comparable to other existing data on neonatal brain mass in western lowland gorillas, with reported values of 227 g [Martin, 1983; Sacher & Staffeldt, 1974] and 217 g [DeSilva & Lesnik, 2008]. Together, data from gorillas, chimpanzees, bonobos, and orangutans (summarized in Table III) suggest that all great apes have relatively mature brains at birth compared to humans, for which reported PBM at birth is approximately 27% of the adult mean brain size [Robson & Wood, 2008]. Given the paucity of available neonatal brain mass data for great ape species, the extent to which Virunga mountain gorillas may or may not differ in PBM at birth from other great apes is a subject for further study. However, results of the current analysis contribute to this discussion by demonstrating more variation in postnatal brain growth strategies among great apes, which warrants further consideration.

Brain Growth and Life History Diversity among Hominoids

The manner in which primates vary the rate and duration of brain growth is proposed to underlie important differences in life history [Barrickman et al., 2008; Barton & Capellini, 2011; Leigh, 2004; Leigh & Bernstein, 2006]. In a comparative examination of brain mass ontogeny in primates, Leigh [2004] recognized two alternative brain growth patterns that are suggested to reflect maternal metabolic strategies. In the first strategy, late ages at reproductive maturation and large adult size confer energetic benefits to mothers, enabling significant early investment in offspring brain growth during the prenatal and early postnatal periods. Offspring of these mothers are born with relatively large brains, and they reach adult brain size early in development. Alternatively, early reproductive maturation and small maternal size, traits favored for their demographic advantages, are associated with a second strategy, in which brain growth shifts to the postnatal period, when the offspring or other group members may help

TABLE III. Neonatal Brain Mass Data from Great Apes

Species	Neonatal brain mass (g)	*N*	Percentage of adult brain mass at birth	References
Gorilla beringei beringei	208	1	42	This study
Gorilla gorilla	227	?	56	Sacher and Staffeldt [1974], Schultz [1965]
	217	1	42	DeSilva and Lesnik [2008]
Pan troglodytes	128	2	36	Sacher and Staffeldt [1974] Schultz [1941]
	151	22	40	DeSilva and Lesnik [2008]
	137	3	36	Herndon et al. [1999], Robson and Wood [2008]
Pan paniscus	155	1	41	DeSilva and Lesnik [2008]
Pongo pygmaeus	129	?	38	Sacher and Staffeldt [1974], Schultz [1941]
	170	3	–	Martin [1983]
	165	3	39	DeSilva and Lesnik [2008]

Note: "Neonatal" is defined differently in the studies that provide these data. DeSilva and Lesnik [2008] describe this period as being within the first week after birth; Robson and Wood [2008] define it as the first 10 days after birth; Sacher and Staffeldt [1974] define it as "shortly after birth."

TABLE IV. Comparison of Life History Characteristics of Select African Great Ape Populations and Modern Humans

Species	Adult female body mass (kg)	Adult brain mass (g)	Age at first birth (years)	Gestation length (days)	Age at weaning (years)	Interbirth interval (years)
Mountain gorillas (Karisoke)	97.7	479	9.9	254–255	2.5–3.7	4
(*Gorilla beringei beringei*)	(1)	(2)	(1)	(4)	(5)	(6)
Eastern chimpanzees	31.3	384	15.2	225.3	5	5.2
(*Pan troglodytes schweinfurthii*)	(3)	(7)	(8)	(9)	(10)	(9)
Modern humans	45.5	1352	19.5	270	2.8	3.7
(*Homo sapiens*)	(7)	(7)	(7)	(7)	(7)	(7)

Note: Nonhuman primate data are derived from different sources, and represent the population central tendency as mean or median except where ranges are provided. All data for eastern chimpanzees are from Gombe, except for adult brain mass. Modern human populations are highly variable in life history parameters, such as age at weaning; data shown here are summarized from Table II in Robson and Wood [2008] and represent modern human foraging groups. Data sources are indicated by the italicized number underneath each value.
(1) Morris et al. [2011]; (2) this study; (3) Morris et al. [2011], Pusey et al. [2005]; (4) Czekala and Sicotte [2000], Harcourt et al. [1980]; (5) Fletcher [2001]; (6) Robbins et al. [2006]; (7) Robson and Wood [2008]; (8) Morris et al. [2011]; (9) Wallis [1997]; (10) Pusey [1983].

subsidize the costs. Offspring of these mothers are born with relatively small brains, and exhibit slow postnatal brain growth and later ages at adult brain size.

As Leigh [2004] noted, however, it is not clear how large-bodied hominoids fit into this framework. Our data from mountain gorillas are more consistent with the first strategy, in which the energetic benefits of large maternal size may allow mothers to invest more heavily in offspring brain growth during the prenatal period, obtaining an absolutely large neonatal brain size and a relatively high proportion of adult brain size before birth. Available neonatal brain mass data suggests that other great apes may also be characterized by increased investment in prenatal brain growth, compared to humans (Table III). However, in humans and chimpanzees, where more detailed ontogenetic data are available, large maternal size and late age at reproductive maturation are coupled with a brain growth strategy characterized by a longer duration of brain size enlargement during postnatal ontogeny compared to mountain gorillas. In chimpanzees, brain size growth is completed between 4 and 5 years of age [Herndon et al., 1999; Neubauer et al., 2012]. Not only do humans allocate a greater proportion of their brain growth to the postnatal period than do both chimpanzees and mountain gorillas [DeSilva & Lesnik, 2008; Simpson et al., 2008], they also incur the costs of substantially higher brain growth rates than chimpanzees during the first 18 months following birth [Leigh, 2004; Robson & Wood, 2008]. The observed pattern in Virunga mountain gorillas, the least frugivorous of the great apes, greatly increases what we know of diversity in brain growth strategy. Detailed examination of diet and other ecological factors that likely influence maternal energetics and allocation of brain growth during the pre- and postnatal periods warrants further attention in hominoids.

Earlier attainment of adult brain size in Virunga mountain gorillas is consistent with other life history characteristics of this population. Despite their absolutely larger bodies and brains, Virunga mountain gorillas are characterized by younger ages at first birth, earlier ages at weaning, and shorter interbirth intervals compared to other hominoids (Table IV). These differences have been attributed to the increased folivory/herbivory of mountain gorillas [Breuer et al., 2009; Janson & van Schaik, 1993; Leigh, 1994; Robbins et al., 2009; Watts & Pusey,

1993]. In contrast to other great apes, Virunga mountain gorillas incorporate very little fruit in their diet. Instead, they rely heavily on terrestrial herbaceous vegetation that is rich in crude protein and readily available year-round in their habitat, apart from the seasonal use of bamboo shoots by some groups [Fossey & Harcourt, 1977; McNeilage, 2001; Rothman et al., 2008, 2007; Watts, 1984, 1996].

The metabolic risk aversion hypothesis posits that frugivorous primates relying on more seasonally available food resources will be selected to grow at low rates, thus reducing their daily energetic needs and distributing the costs of growth over a longer juvenile period; this strategy reduces the risk of starvation associated with elevated feeding competition. A corollary to this hypothesis is that reliance on abundant and perennially available food resources is expected to be associated with higher growth rates and earlier ages at maturity [Janson & van Schaik, 1993; Leigh, 1994; Leigh, 1995; Leigh & Shea, 1995, 1996]. This has been proposed to explain the higher body mass growth velocities of gorillas compared to other great apes [Leigh, 1994; Leigh & Shea, 1995, 1996], and the earlier age of reproductive maturation in mountain gorillas compared to western lowland gorillas [Breuer et al., 2009]. Results of the current study suggest that reliance on a more herbivorous and protein-rich diet, together with the energetic advantages of large maternal size [Leigh, 2004], may enable a life history strategy in which body, brain, and reproductive maturation are more tightly linked in mountain gorillas than they are in some other taxa [Pereira & Leigh, 2003]. A component of this strategy is that mountain gorilla females support the higher costs of rapid offspring brain growth during the prenatal and early postnatal periods, such that their infants reach adult brain size around the time of weaning at approximately 3 years of age [Fletcher, 2001; Fossey, 1979]. It is also notable that gorilla mothers generally, and mountain gorilla mothers in particular, produce milk that is higher in crude protein content and percent energy derived from protein than milk produced by chimpanzee and bonobo mothers [Hinde & Milligan, 2011]. Mountain gorilla mothers also produce milk that is comparatively high in α-linolenic acid (18:3n-3; ALA), which is a precursor of the omega-3 fatty acid docosahexaenoic acid (DHA), an important building block for neural development and function [Hinde & Milligan, 2011; Milligan et al., 2008; Whittier et al., 2011]. However, the contribution of high ALA content in mountain gorilla milk to postnatal brain growth is uncertain because anthropoids are inefficient at converting ALA to DHA [Milligan & Bazinet, 2008].

Social Learning

Differences among hominoid taxa in the social learning of foraging behavior may also relate to diversity in brain growth patterns. Early completion of brain growth in mountain gorillas might limit the degree to which social learning has the opportunity to shape behavioral flexibility as compared with other great apes. While regional traditions in behaviors and tool use are well documented among wild chimpanzees and orangutans [Bastian et al., 2010; Lycett et al., 2010; van Schaik et al., 2003; Whiten et al., 1999], evidence for social transmission of behavior in gorillas is more scarce [Stoinski et al., 2001]. Because mountain gorillas have dental and gut specializations that allow them to process a greater amount of fibrous material from leaves, they are not as heavily dependent on learning foraging routes for seasonal fruit, nor do they require tools to extract nuts and insects. Consequently, while widespread in chimpanzees, tool use is rarely observed in wild gorillas and appears to be largely unrelated to food processing [Breuer et al., 2005]. Furthermore, although it has been argued that the processing of stinging nettles by mountain gorillas requires skills that need to be learned from observing others [Byrne et al., 2011], Tennie et al. [2008] contend that social learning plays a limited role in this behavior.

In contrast, it has been demonstrated that proficiency in termite fishing among Gombe chimpanzees takes many years to develop (up to 4–5 years of age), and the rate of skill acquisition in juveniles is related to maternal behavior [Lonsdorf, 2006]. Such tool-related behaviors and other complex cognitive skills are typically acquired over a long juvenile period; during this life history phase, developmental changes in synaptic connectivity and myelination facilitate a greater degree of plasticity in learning [Bufill et al., 2011]. It is possible that the abundant availability of food resources that do not require extractive technologies to access or sophisticated metal maps to locate, may therefore lessen the need for an extended learning period related to slow brain development in mountain gorillas. Data on microstructural or molecular ontogenetic changes in the cerebral cortex of gorillas compared to chimpanzees would help to resolve whether such modifications track the trajectory of overall brain size growth.

CONCLUSIONS AND FUTURE DIRECTIONS

The current study demonstrates that Virunga mountain gorillas reach adult brain size early compared to chimpanzees and modern humans, and underscore the need for ontogenetic data from all hominoid taxa, including other gorilla subspecies. Without such data, our understanding of links between hominoid brain growth strategies and variation in life history, diet, and other environmental factors in the wild is limited. Interestingly, we found that adult Virunga mountain gorillas that died in the late 1960s to early 1980s had significantly smaller

brain sizes that those that have died more recently (postdating the mid-1990s). It is possible that more recent conservation efforts led by local governmental and nongovernmental organizations have produced an environment of lower stress for Virunga mountain gorillas. Intensification of protection and monitoring efforts focused on this population over the past two decades is associated with a reduction in gorilla deaths from poaching and injury (e.g., from snares set for other prey), and increased detection and treatment of habituated gorillas for respiratory disease and other human-induced life-threatening conditions [Robbins et al., 2011]. The population size has also increased over the same time period, with habituated gorillas experiencing higher population growth rates than unhabituated gorillas [Robbins et al., 2011]. The potential effects of stress on mountain gorilla brain development may be significant. Many damaging effects of stress on the brain have been described, particularly during development, through activity of the fetal hypothalamic-pituitary-adrenal axis [Lupien et al., 2009]. The hippocampus appears to be especially sensitive to such effects, with many studies indicating hippocampal atrophy following stress exposure [Bremner, 1999; Sapolsky, 1996]. We are currently undertaking MRI-based analyses of mountain gorilla brains to examine volumetric variation in neural structures which may be associated with stress, development, and aging. Future studies incorporating genetic relatedness and locality data within the Virungas may shed light on whether the observed temporal differences in adult brain size among mountain gorillas reported here might be the result of spatial or temporal variability in human-related impacts, diet, body size, or other factors [Grueter et al., 2010; McNeilage, 2001; Watts, 1984].

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