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Facial asymmetry tracks genetic diversity among *Gorilla* subspecies

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Mountain gorillas are particularly inbred compared to other gorillas and even the most inbred human populations. As mountain gorilla skeletal material accumulated during the 1970s, researchers noted their pronounced facial asymmetry and hypothesized that it reflects a population-wide chewing side preference. However, asymmetry has also been linked to environmental and genetic stress in experimental models. Here, we examine facial asymmetry in 114 crania from three *Gorilla* subspecies using 3D geometric morphometrics. We measure fluctuating asymmetry (FA), defined as random deviations from perfect symmetry, and population-specific patterns of directional asymmetry (DA). Mountain gorillas, with a current population size of about 1000 individuals, have the highest degree of facial FA (explaining 17% of total facial shape variation), followed by Grauer gorillas (9%) and western lowland gorillas (6%), despite the latter

experiencing the greatest ecological and dietary variability. DA, while significant in all three taxa, explains relatively less shape variation than FA does. Facial asymmetry correlates neither with tooth wear asymmetry nor increases with age in a mountain gorilla subsample, undermining the hypothesis that facial asymmetry is driven by chewing side preference. An examination of temporal trends shows that stress-induced developmental instability has increased over the last 100 years in these endangered apes.

1. Background

Facial symmetry is widely regarded as a reliable indicator of attractiveness and reproductive success in humans, while asymmetry is often used as a measure of early life stress [1,2]. As both sides of bilaterally symmetric faces share the same genotype, it is expected that they will exhibit the same phenotype, except when individuals experience instability during development [2]. Therefore, studies typically use fluctuating asymmetry (FA) as a measure of individual or population-level fitness, calculated as the random deviations from perfect symmetry or from population-specific patterns of directional asymmetry (DA) [2,3]. Most FA studies have focused on elucidating the environmental causes, although there is also evidence suggesting that FA is heritable [4,5]. Experimental studies have linked environmental stressors and inbreeding to the level of FA in bilateral structures of rodents and flies [6–8]. In humans, it has been suggested that genetic or environmental stress increases susceptibility to health problems later in life, such that FA might provide a reliable signal of fitness [9]. As a result, studies measuring FA in non-human primate faces have focused on the link between FA and adult fitness or health outcomes [10], and not necessarily the environmental conditions under which individuals developed. As such, the possible stressors behind facial FA beyond the classical 'environmental or genetic' dichotomy remain poorly understood. Moreover, surprisingly little is known about the evolutionary significance of facial asymmetry, including the magnitude of facial FA in extinct hominins and our closest living relatives, the non-human apes [11,12].

Groves & Humphrey [13] first described the marked asymmetry present in the craniofacial skeletons of Virunga mountain gorillas (*Gorilla beringei beringei*) studied at the Dian Fossey Gorilla Fund's Karisoke Research Center (figure 1). They found that western lowland gorilla (*G. gorilla gorilla*) faces were not significantly asymmetric (*n* = 138), but 19 of 55 eastern gorillas (i.e. mountain and Grauer (*G. beringei graueri*)) had faces that were at least 4 mm longer on the left side than the right, and of these individuals, 18 were Virunga mountain gorillas. Mountain gorillas were the only subspecies with almost as many asymmetric as symmetric individuals in the sample, and the authors suggested that the observed asymmetry may reflect a preference for chewing on the left side [13]. This 'gross asymmetry' was further evidenced by the presence of uneven tooth wear and lopsidedness of the sagittal crest, but they acknowledged that other closely related taxa with equally developed masticatory musculature, such as orangutans, did not seem to show similar levels of facial asymmetry. Indeed, while habitual unilateral chewing is commonly invoked as an explanation for facial asymmetry [14], this link has largely been assumed rather than tested.

In this study, we use three-dimensional geometric morphometrics to quantify adult facial skeleton asymmetry in three gorilla subspecies with well-documented variation in environmental (extrinsic) and genetic (intrinsic) stress, namely western lowland gorillas, Grauer gorillas and Virunga mountain gorillas (figure 2). Although we are not directly measuring genetic or environmental variables, we use the term 'stress' to describe the factors hypothesized to increase developmental instability, thus leading to measurable facial asymmetry in the skeleton. In addition to FA, we also analyse DA, which occurs when one side differs consistently from the other at the population level, in line with the differential chewing hypothesis proposed by Groves & Humphrey [13]. We test whether the marked asymmetry in mountain gorillas is significantly greater than that expressed by other gorilla taxa, and evaluate the results considering current ecological, behavioural, and genetic information. Because asymmetric variation usually only explains a small proportion of the total variation in morphological analyses, we also characterize symmetric variation in facial morphology, as well as subspecies-level variation in facial asymmetry as it relates to sexual dimorphism. We investigate three alternative hypotheses to test whether genetic stress, environmental stress, or chewing side preference better correspond with facial asymmetry among gorilla subspecies.

First, we test whether more inbred gorilla subspecies exhibit more pronounced facial FA. In terms of genetic stress or inbreeding, mountain gorillas are homozygous at about one third of their genomes, and thus have very low genetic diversity compared to western lowland and, to a lesser extent, Grauer gorillas [16,17]. Mountain gorillas are more inbred than even the most inbred contemporary human populations [18] and the Altai Neanderthal [19]. While several studies have suggested that inbreeding might lead to higher levels of FA in model species [8], this study provides an opportunity to assess facial FA in the case of extreme inbreeding yet relatively stable socioecological conditions of the mountain gorilla.

Second, we assess whether gorillas that experience more environmental stress exhibit more pronounced facial FA. While environmental stress encompasses many factors, one main axis of variation among gorilla subspecies lies in dietary and ecological variability, with western lowland gorillas being exposed to the highest level of seasonal unpredictability in food resources and competition [20]. Western lowland gorillas have also experienced major population declines due to human activity and infectious diseases, most notably Ebola, resulting in approximately 90% casualties in affected populations [21]. By contrast, Virunga mountain gorillas eat a reliable, almost entirely folivorous diet, and have experienced increased population growth over the past several decades [22]. Grauer gorillas fall between these two extremes, with those from highland areas eating a more folivorous diet, and those from lowland areas eating a similar proportion of fruit as western lowland gorillas [20,23]. Grauer gorillas have also experienced major population declines in the last century, losing up to 77% of their total population [24]. In terms of gorilla behavioural ecology, these dietary and other social differences form potential sources of variation in environmental stress among taxa.

Third, we test whether gorillas exhibit more pronounced facial asymmetry because they have a chewing side preference.

Figure 1. An extreme example of facial asymmetry in a female Virunga mountain gorilla cranium (Tayna, individual GP.148), shown as a three-dimensional surface model with texture. This individual was not included in the sample because she was dentally immature at the time of death, but she exhibits an extreme version of the asymmetric pattern documented in this study. (Online version in colour.)
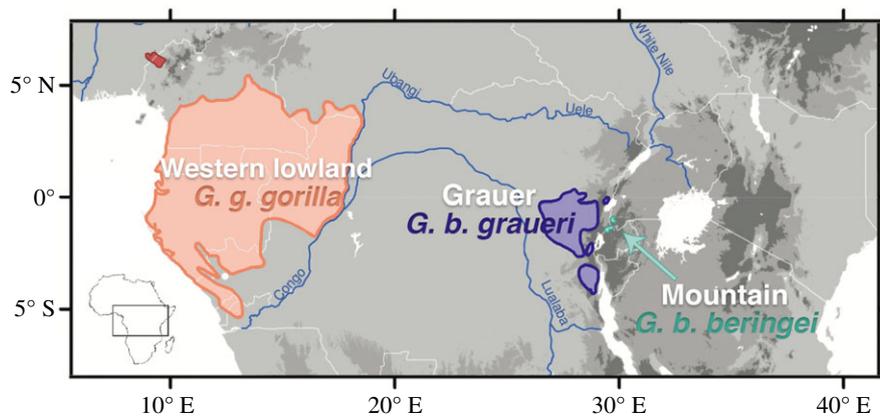

Figure 2. The approximate ranges of the four *Gorilla* subspecies. The three subspecies analysed in this study are labelled (western lowland gorillas, Grauer gorillas and mountain gorillas), while cross river gorillas (*G. g. diehli*) are shown in red at the top left corner of the map. Major river boundaries (blue), elevation grades (grey) and country borders (white) are also shown. Modified from Tocheri *et al.* [15]. (Online version in colour.)

If gorillas preferentially chew on one side of the mouth, then they can be expected to show differences in the degree of tooth wear between the left and the right sides, which will match the pattern in facial asymmetry. A subsample of Virunga mountain gorillas with associated tooth wear data are used to test whether they exhibit chewing side preferences as evidenced by uneven tooth wear, and the patterns of facial asymmetry are considered in light of those results.

2. Material and methods

The sample includes the crania of 40 Virunga mountain gorillas (*Gorilla beringei beringei*), 40 Grauer gorillas (*G. beringei graueri*) and 34 western lowland gorillas (*G. gorilla gorilla*), with equal representation of females and males. We analysed adult individuals as determined by the third permanent molar being fully erupted and in occlusion. Only those with completely preserved facial anatomy, and no clear evidence of trauma or pathology, were included. In the mountain gorilla sample, 22 of the individuals were from the Mountain Gorilla Skeletal Project (Musanze, Rwanda) and three-dimensional models were digitized with a Breuckmann SmartScan white light scanner (aligned and merged in Optocat software v.11.01.06-2206). The remaining 92 models were reconstructed from medical CT scans at the Katholieke Universiteit Leuven, Belgium (Siemens Sensation 64,

120 kV, 135 mA, 1 mm slice thickness, reconstruction interval of 0.5 mm, 15 cm field of view, 0.29296875 mm pixel size, 512*512 pixel matrix) [25], and the Smithsonian's National Museum of Natural History (Washington, DC; Siemens Somatom Emotion CT Scanner, 110 kV, 70 mA, 1 mm slice thickness, 0.1 mm reconstruction increment; surface models generated in Materialize Mimics). A recent study suggests that there are no significant differences in models derived from different imaging modalities [26], allowing for the direct comparisons made here.

We used Viewbox 4 software (http://www.dhal.com/) to place 156 homologous landmarks and curve sliding semilandmarks on the cranial models (electronic supplementary material, figure S1). The landmark configuration uses classic fixed facial landmarks supplemented by curve sliding semilandmarks set on the face and palate. Because of the uncertainty in semilandmark location, they were slid along their corresponding curves with respect to the fixed landmarks in order to minimize bending energy following a standard procedure for semilandmark analyses [27]. Landmarks were digitized twice on each individual to assess FA and parse it out from measurement error via Procrustes ANOVA, as described below. The raw three-dimensional coordinates were subjected to Procrustes superimposition to remove the effect of scale, orientation and position from the shape analyses [28]. The symmetric versus asymmetric components of shape variation were then analysed separately: the symmetric component comprised the original and mirrored landmark configurations for each cranium, while the asymmetric

Table 1. Interspecific Procrustes ANOVAs of gorilla facial morphology. SS, sum of squares; MS, mean squares (multiplied by 1000); d.f., degrees of freedom; F, F-ratio; p: p-value; %var, percentage of variance explained by each effect; S, symmetry; DA, directional asymmetry; FA, fluctuating asymmetry. Asterisks mark significant differences among taxa, as determined by 1000 bootstraps of observed FA correlation matrices (see electronic supplementary material, table S3 for details).

taxon	effect	SS	MS*	d.f.	F	p	%var
mountain gorillas (*G.b.b.*)	individual (S)	0.2178	0.240	9087	4.61	<0.001	79.1
n = 40	side (DA)	0.0055	0.242	228	4.65	<0.001	2.0
	ind × side (FA)	0.0463	0.052	8892	19.99	<0.001	16.8*
	measurement error	0.0048	0.003	18 440			1.7
	total	**0.2755**					
Grauer gorillas (*G.b.g.*)	individual (S)	0.2254	0.248	9087	9.92	<0.001	88.1
n = 40	side (DA)	0.0015	0.067	228	2.69	<0.001	0.6
	ind × side (FA)	0.0222	0.025	8892	8.07	<0.001	8.7*
	measurement error	0.0057	0.003	18 440			2.2
	total	**0.2559**					
western lowland gorillas (*G.g.g.*)	individual (S)	0.2123	0.276	7689	14.54	<0.001	91.1
n = 34	side (DA)	0.0017	0.074	228	3.91	<0.001	0.7
	ind × side (FA)	0.0143	0.019	7524	7.93	<0.001	6.1*
	measurement error	0.0038	0.002	15 674			1.6
	total	**0.2331**					

component includes deviations of the original configurations from the symmetric averages [29–32]. Principal component analysis was conducted to analyse the main patterns of variation using symmetric coordinates and asymmetric residuals. The effects of allometry were assessed using a multivariate regression of shape versus centroid size. Analyses of the different components of variance were conducted using Procrustes ANOVA [29], in which the factor 'individual' represents symmetric variation, 'side' represents one-sided or DA, and the interaction between the two represents non-directional or FA. Measurement error was calculated as the residual variation in the Procrustes ANOVA, and explains between 1.6 and 2.2% of the shape variation (table 1).

To test for differences in the magnitude of facial FA among taxa, we conducted a bootstrapping analysis of the correlation matrices for the FA component following Webster & Zelditch [33]. The probability of matrices being identical was assessed by 1000 bootstraps (unpublished R code from Haber, provided by Webster & Zelditch [33]). Individual facial asymmetry scores were calculated with respect to a perfectly symmetric configuration to measure the magnitude of asymmetry across the whole face. This was done by calculating the Procrustes distance between the original and reflected and relabelled landmark configurations following Procrustes registration [2]. Individual asymmetry scores were compared to the magnitude of tooth wear asymmetry because there was no clear population-level chewing side preference (figure 4). If there had been a clear directional signal in tooth wear, directional facial asymmetry would have been the more appropriate form of asymmetry to assess in relation to tooth wear.

In a subsample of Virunga mountain gorillas (sample sizes specified in each table and figure), we assessed the relationships between tooth wear asymmetry in upper and lower molars of the same position (electronic supplementary material, table S4), facial asymmetry scores and molar wear asymmetry (electronic supplementary material, table S5; figure 4), the relationship between each variable and age at death (electronic

supplementary material, figure S2), and facial asymmetry scores through time (figure 4) using Spearman's rank correlation analysis. We compared the magnitude and direction of tooth wear in upper versus lower molars of the same position as a test of whether this metric is consistent and a reliable indicator of chewing side preference. Tooth wear was assessed by calculating the per cent of dentine exposure in the first permanent molars following Galbany et al. [34]. The percentage of the occlusal surface with exposed underlying dentine, relative to the total area of the occlusal surface, was measured in both the right and left first, second and third molars using digital photographs of original teeth. While a three-dimensional topographic measure of tooth wear, such as slope, is more sensitive to early stages of tooth wear [35], dentine becomes exposed on the M1 in mountain gorillas by the time the M3 erupts [34], and thus percentage of exposed dentine is sensitive enough to capture molar wear in this adult sample of gorillas. Known ages at death are available for a majority of the mountain gorilla individuals included in the subsample, but those without known ages were estimated based on incisor wear following the protocol developed by Galbany et al. [36], which estimates ages at death within about a 1–3 year error margin (see electronic supplementary material, figure S2 for sample details). The collection dates were known for most individuals in the sample, but in cases where there were several years in which remains were estimated to have been collected, we used the earliest possible date for our analysis. For example, 20 Grauer gorillas were collected between 1980 and 1984, so we used 1980. Ten mountain gorillas were also collected in estimated windows of 5 years (4 individuals) and 9 years (5 individuals), with one individual only being known to have been collected before 2001, so we substituted the year 2000 in that instance. Besides the known individuals with uncertain collection dates, there is likely some additional variation in record keeping across institutions, as well as collection practices over time, justifying our estimation and inclusion of the uncertain dates in this study. To assess the trend in facial asymmetry magnitude through time, we conducted a linear mixed model with
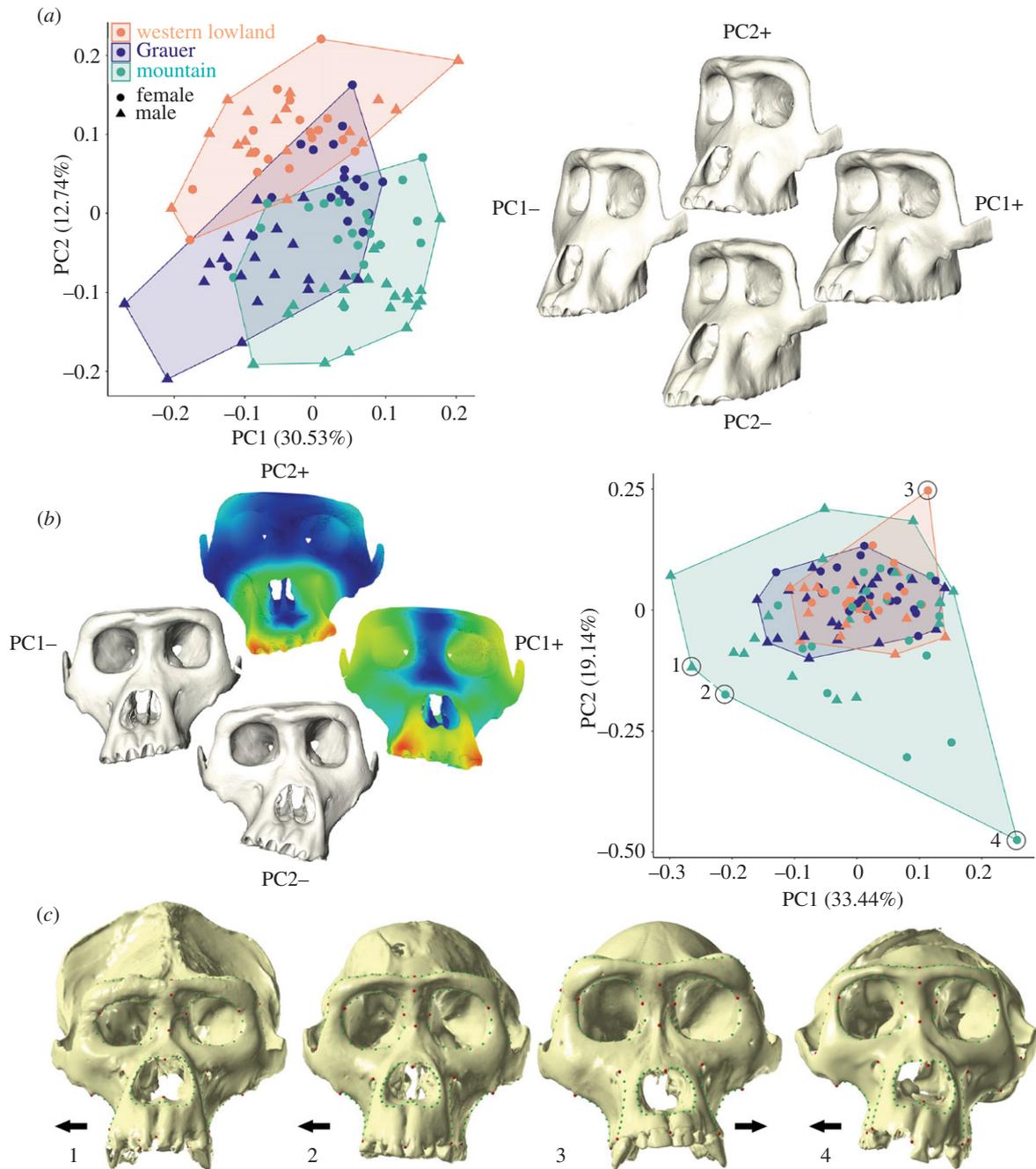
Figure 3. Facial shape variation in gorillas. (*a*) Principal component analysis (PCA) of the symmetric component of facial shape variation. Three-dimensional surface models of the mean shape warped along the positive and negative PC1 and PC2 axes. (*b*) PCA of the asymmetric component, with three-dimensional models of the mean shape warped along the positive and negative axes. Two models show distance-based heatmaps of the intensity of asymmetry across the face with red indicating more asymmetry and blue indicating less asymmetry. In the PCA, specific individuals are circled and shown in panel (*c*), which depicts actual surface models of the most asymmetric individuals. Arrows denote directionality of asymmetry in the lower midface. Green and red points represent fixed and sliding semilandmarks used in this study, respectively. (Online version in colour.)

collection date as a fixed effect and sex class (sex and subspecies) as a random effect in order to control for differences in the level of asymmetry among groups.

Analyses were carried out in MorphoJ and R (v. 4.0.0) [37].

3. Results

The principal component analyses (PCAs) and Procrustes ANOVAs of the symmetric (i.e. the original and mirrored landmark configurations for each cranium) and asymmetric (i.e. deviations of the original configurations from the symmetric averages) aspects of shape variation show that 79–

91% of shape differences within and among gorilla taxa are related to symmetric variation in facial morphology (figure 3*a*, table 1). The plot of the first (PC1) and second (PC2) principal components of the symmetric aspect, which explain 30.5% and 12.7% of the variance, respectively, shows separation of western lowland and mountain gorillas within the morphospace, mainly along PC2, with Grauer gorillas falling in between but overlapping more with mountain gorillas (figure 3*a*). In general, western lowland gorillas have relatively narrower, less prognathic faces with more rounded orbits framed by a curved supraorbital torus. By contrast, mountain gorillas have relatively broader, more prognathic faces and more rectangular orbits framed by a flat
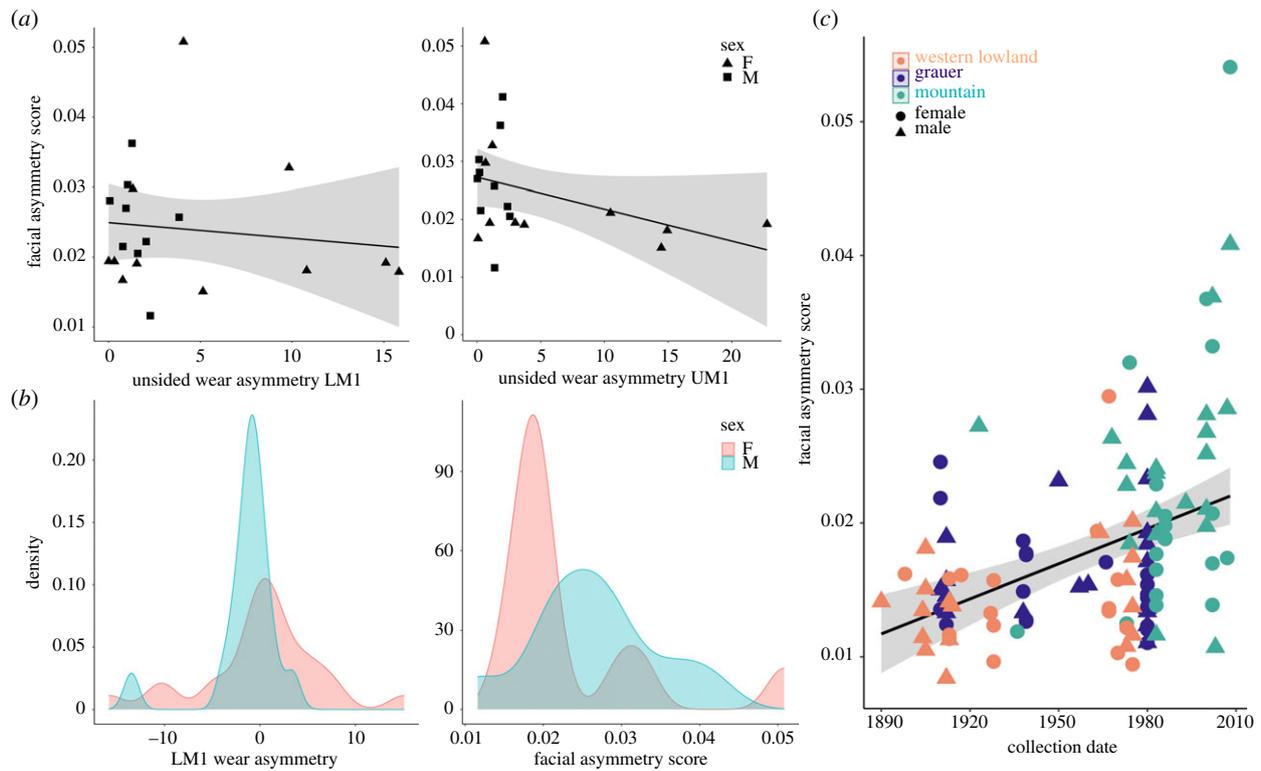
Figure 4. (a) Regressions of unsided tooth wear asymmetry in lower first molars (LM1, n = 20) (r_s = −0.19, p = 0.422) and upper first molars (UM1, n = 21) (r_s = −0.43, p = 0.054) versus facial asymmetry scores in the Virunga mountain gorilla subsample. Shading shows 95% confidence intervals. (b) Density plots of tooth wear asymmetry of LM1 (n = 41) and facial asymmetry scores (n = 22) in Virunga mountain gorillas. At left, positive values indicate greater LM1 wear on the right side, while negative values indicate greater LM1 wear on the left side. At right, larger numbers denote greater facial asymmetry overall. (c) Facial asymmetry scores of individual western lowland, Grauer and mountain gorillas (n = 114). Facial asymmetry increases through time when controlling for sex and species differences in the magnitude of asymmetry ($F_{1,107}$ = 4.95, p = 0.028). Grey shading shows 95% confidence intervals. (Online version in colour.)

supraorbital torus. Grauer gorillas have the narrowest faces of the three taxa, rounder orbits, and a taller nasal aperture and rostrum. When sex is considered, male and female mountain gorillas separate primarily along PC2, while male and female Grauer gorillas separate along PC1 and PC2 (figure 3a). By contrast, male and female western lowland gorillas do not clearly separate along either of the first two PCs (figure 3a), nor PC3 (not shown). The multivariate regression of shape against size indicates that allometry explains about 10% of the shape variation in the symmetric aspect (r = 0.10; p < 0.001), and 15% (r = 0.38; p < 0.001) and 8% (r = 0.28; p = 0.002) for PC1 and PC2, respectively.

The PCA of the asymmetric aspect of shape shows that the range of variation in mountain gorillas envelops that of the other two taxa (figure 3b). Both DA and FA are highly significant in all three taxa (table 1), but FA explains a much larger proportion of variation, ranging from 6% in western lowland gorillas, to 9% in Grauer gorillas, and 17% in mountain gorillas compared to the 0.6–2.0% of shape variation explained by DA. The probability of observed FA correlation matrices being identical between each of the three taxa, as assessed by 1000 bootstraps, is 0, suggesting that mountain gorillas have significantly greater facial FA than both Grauer and western lowland gorillas, and that Grauer gorillas have significantly greater FA than western lowland gorillas (table 1; electronic supplementary material, table S3). To assess whether these results are related to the drastic reduction of gorilla habitat and population sizes, the collection years of the individuals (ranging from 1880 to 2008) were compared to facial asymmetry scores. The magnitude of facial asymmetry for each individual increases through

time within the combined sample, even when controlling for sex and species differences in the magnitude of asymmetry ($F_{1,107}$ = 4.95, p = 0.028). The most recent mountain gorillas exhibit the highest facial asymmetry scores of all (figure 4).

Though statistically significant in all three taxa, DA only explains a small percentage of morphological variation (0.6–2.0%), suggesting that it is not a major factor shaping facial morphology at the population level in gorillas (table 1). In all three taxa, most of the total asymmetry occurs in the lower midface, as shown in several examples of particularly asymmetric individuals (figure 3c), and in distance-based heatmaps summarizing the asymmetry of the whole sample (figure 3b). In the Virunga mountain gorilla subsample, we found that the upper and lower molars (UM and LM) of the same position (i.e. first, second or third) exhibit matching unsided wear (electronic supplementary material, table S4), but there is no relationship between unsided tooth wear asymmetry (i.e. considering only the magnitude) and facial asymmetry scores (electronic supplementary material, table S5, figure 4). In other words, individuals with the highest degree of differential wear between the left and the right side do not show the highest level of facial asymmetry.

Male Virunga mountain gorillas, which tend to be younger than females in this subsample, show less variation in right–left tooth wear differences compared to females (figure 4). However, there is no evidence of chewing side preference as inferred from tooth wear asymmetry within this population; distributions of tooth wear asymmetry centre close to 0 in all six teeth examined (figure 4 shows density plot for LM1). Older individuals exhibit more asymmetric tooth wear compared to younger individuals (r_s = 0.56,

fragmentation thresholds for management. *Evol. Appl.* **7**, 506–518. (doi:10.1111/eva.12154)

40. Caillaud D, Levréro F, Cristescu R, Gatti S, Dewas M, Douadi M, Gautier-Hion A, Raymond M, Ménard N. 2006 Gorilla susceptibility to Ebola virus: the cost of sociality. *Curr. Biol.* **16**, R489–R491. (doi:10.1016/j.cub.2006.06.017)

41. Plumptre AJ, Nixon S, Kujirakwinja DK, Vieilledent G, Critchlow R, Williamson EA, Nishuli R, Kirkby AE, Hall JS. 2016 Catastrophic decline of world's largest primate: 80% loss of Grauer's gorilla (*Gorilla beringei graueri*) population justifies Critically Endangered status. *PLoS ONE* **11**, e0162697. (doi:10.1371/journal.pone.0162697)

42. Barks SK *et al.* 2014 Variable temporoinsular cortex neuroanatomy in primates suggests a bottleneck effect in eastern gorillas. *J. Comp. Neurol.* **522**, 844–860. (doi:10.1002/cne.23448)

43. Maisels F, Bergl RA, Williamson EA. 2018 *Gorilla gorilla* (amended version of 2016 assessment). *The IUCN Red List of Threatened Species 2018*. (doi:10.2305/IUCN.UK.2018-2.RLTS.T9404A136250858.en)

44. Sapolsky RM, Romero LM, Munck AU. 2000 How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev.* **21**, 55–89. (doi:10.1210/edrv.21.1.0389)

45. Ostrofsky KR, Robbins MM. 2020 Fruit-feeding and activity patterns of mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda. *Am. J. Phys. Anthropol.* **163**, 3–20. (doi:10.1002/ajpa.24056)

46. McFarlin SC *et al.* 2013 Early brain growth cessation in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Am. J. Primatol.* **75**, 450–463. (doi:10.1002/ajp.22100)

47. McGrath K, El Zaatari S, Guatelli-Steinberg D, Stanton MA, Reid DJ, Stoinski TS, Cranfield MR, Mudakikwa A, McFarlin SC. 2018 Quantifying linear enamel hypoplasia in Virunga Mountain gorillas and other great apes. *Am. J. Phys. Anthropol.* **166**, 337–352. (doi:10.1002/ajpa.23436)

48. Al Kaissi A, Chehida FB, Gharbi H, Ghachem MB, Grill F, Varga F, Klaushofer K. 2007 Persistent torticollis, facial asymmetry, grooved tongue, and dolicho-odontoid process in connection with atlas malformation complex in three family subjects. *Eur. Spine J.* **16**, 265–270. (doi:10.1007/s00586-006-0297-3)

49. Akbari MR, Nejad MK, Askarizadeh F, Pour FF, Pazooki MR, Moeinitabar MR. 2015 Facial asymmetry in ocular torticollis. *J. Curr. Ophthalmol.* **27**, 4–11. (doi:10.1016/j.joco.2015.10.005)

50. Collard M, Wood B. 2000 How reliable are human phylogenetic hypotheses? *Proc. Natl Acad. Sci. USA* **97**, 5003–5006. (doi:10.1073/pnas.97.9.5003)

51. Ackermann RR. 2002 Patterns of covariation in the hominoid craniofacial skeleton: implications for paleoanthropological models. *J. Hum. Evol.* **43**, 167–187. (doi:10.1006/jhev.2002.0569)

52. Balolia KL, Soligo C, Lockwood CA. 2013 Sexual dimorphism and facial growth beyond dental maturity in great apes and gibbons. *Int. J. Primatol.* **34**, 361–387. (doi:10.1007/s10764-013-9666-z)

53. Shakarad M, Prasad NG, Rajamani M, Joshi A. 2001 Evolution of faster development does not lead to greater fluctuating asymmetry of sternopleural bristle number in *Drosophila*. *J. Genet.* **80**, 1. (doi:10.1007/BF02811412)

54. Galbany J, Abavandimwe D, Vakiener M, Eckardt W, Mudakikwa A, Ndagijimana F, Stoinski TS, McFarlin SC. 2017 Body growth in wild mountain gorillas (*Gorilla beringei beringei*) from Volcanoes National Park, Rwanda. *Am. J. Phys. Anthropol.* **163**, 570–590. (doi:10.1002/ajpa.23232)