



Long bone diaphyseal shape follows different ontogenetic trajectories in captive and wild gorillas.

Stephanie L. Canington,^{1*} Adam D. Sylvester,¹ M. Loring Burgess,¹ Juho-Antti Junno,² and Christopher B. Ruff¹

¹Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, MD 21205

²Department of Archaeology, University of Oulu, Oulu, Finland 90014

Running Headline: Captive vs. wild gorilla ontogeny

Keywords: *captivity, great ape, morphology, growth*

Proof to be sent to:

Stephanie L. Canington
Center for Functional Anatomy and Evolution
1830 East Monument St. Room #305
Baltimore, MD 21205
Cell: (847) 826-7666
Fax:

Grant sponsorship:

Access to the mountain gorilla comparative sample was assisted by Shannon McFarlin (The George Washington University) and the Mountain Gorilla Skeletal Project, funded by the National Science Foundation (BCS-0852866, BCS-0964944), National Geographic Society's Committee for Research and Exploration (8486-08), and The Leakey Foundation. Funding for the comparative dataset was provided by two National Science Foundation grants: BCS-0642297 and BCS-1316104 (www.nsf.gov), the Leakey Foundation, and the Wenner-Gren Foundation for Anthropological Research (8657).

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1002/ajpa.23636](https://doi.org/10.1002/ajpa.23636)

ABSTRACT

Objectives: A number of studies have demonstrated the ontogenetic plasticity of long bone diaphyseal structure in response to mechanical loading. Captivity should affect mechanical loading of the limbs, but whether captive apes grow differently than wild apes has been debated. Here we compare captive and wild juvenile and adult *Gorilla* to ascertain whether growth trajectories in cross-sectional diaphyseal shape are similar in the two environments.

Materials and Methods: A sample of young juvenile ($n = 4$) and adult ($n = 10$) captive *Gorilla gorilla gorilla* specimens, with known life histories, were compared with age-matched wild *G.g. gorilla* ($n = 62$) and *G. beringei beringei* ($n = 75$) in relative anteroposterior to mediolateral bending strength of the femur, tibia, and humerus. Cross sections were obtained using peripheral quantitative CT.

Results: Captive and wild adult *G.g. gorilla* differed in bending strength ratios for all three bones, but these differences were not present in young juvenile *G.g. gorilla*. In comparisons across taxa, captive juvenile *G.g. gorilla* were more similar to wild *G.g. gorilla* than to *G.b. beringei*, while captive adult *G.g. gorilla* were more similar in shape to *G.b. beringei* in the hind limb.

Discussion: Captive and wild *G. gorilla* follow different ontogenetic trajectories in long bone diaphyseal shape, corresponding to environmental differences and subsequent modified locomotor behaviors. Differences related to phylogeny are most evident early in development.

INTRODUCTION

Numerous experimental and observational studies have demonstrated the extent to which long bone diaphyseal structure is developmentally plastic, responding to the mechanical forces placed upon it (Biewener and Bertram, 1994; Jones et al., 1977; Lee et al., 2002; O’Connour et al., 1982; Ruff et al., 2006). Thus, among humans and African apes, ontogenetic changes in inter-limb bone strength proportions parallel changes in relative mechanical loading of the limbs during locomotor behavior (Ruff, 2003; Ruff et al., 2013, 2018; Sarringhaus et al., 2016). While systemic factors (e.g., disease or poor nutrition) may also affect diaphyseal cross-sectional morphology (e.g., relative cortical thickness; Garn et al., 1969), movement patterns, or the orientation of loading, are most likely to cause directional changes in cross-sectional shape. Such changes can be quantified using mechanical beam models to calculate relative bending rigidities or strengths in different anatomical planes (Ruff, 2007). A number of studies have documented relationships between these bone parameters and behavioral differences during development (Carlson and Judex, 2007; Cowgill et al., 2010; MacDonald et al., 2009; Shaw and Stock, 2009a,b).

Captivity presents a unique opportunity to further examine the effects of mechanical loading over developmental time. With far less area to exploit within an enclosure, captive primates are often excluded during skeletal data collection for locomotor research studies as they are thought to poorly reflect the natural behaviors and activity levels occurring in the wild (Boorer, 1972; Clarke et al. 1982; Kelley and Garcia, 2010; Less et al., 2012; for a review of behavioral research, see Vereecke et al., 2011). Much of the skeletal research on captive

primates has focused on disease in animal populations of early zoos, highlighting the effects of insufficient vitamin absorption/synthesis (diet or sunlight) on various bone afflictions (e.g., tuberculosis and rickets, Sutton, 1884; osteodystrophia fibrosa, Canington and Hunt, 2016; O'Regan and Kitchener, 2005; also see Strong et al., 2016) and craniofacial and dental defects associated with unusual diets or food processing (Cousins, 1972; Farrell et al., 2015).

Few skeletal studies, however, have directly compared the postcrania of captive and wild primates in a biomechanical context, to test whether behavioral differences resulting from captive and wild environments affect limb bone structural properties. Fleagle and Meldrum (1988) noted that ulnar cross-sectional shape of a zoo-reared *Pithecia pithecia* more closely resembled that of wild *Chiropotes satanus* rather than wild *P. pithecia*, possibly reflecting less frequent suspensory behaviors and more quadrupedal locomotion in the zoo animal. Bello-Hellegouarch et al. (2013) used a landmark-based geometric morphometrics approach to quantify differences in the scapular morphologies of adult captive and wild gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygmaeus*), but reported no significant differences in morphology between captive and wild groups. However, histories (i.e., for how long and at what ages they lived in captivity) were not known for almost half of the captive animals, and some scapular features that have been shown in experimental models to respond to behavior during development (Green et al., 2012) were not assessed. In a study of morphological signals in the ankle related to vertical climbing in Hominidae, Venkataraman et al. (2013) found differences between captive and wild great apes in talar wedging and relative mediolateral breadth of the anterior distal tibial articular surface, which they interpreted to be functionally related to load dissipation during the considerable dorsiflexion of

the foot that occurs during vertical climbing. Similar to other studies comparing captive and wild primates, specific information regarding the period of captivity of their zoo sample is not given.

Lewton (2017) recently reported results of a comparison of long bone articular surface areas between adult captive and wild chimpanzees. All captive animals had been in captivity since infancy. Although a few differences between captive and wild samples were found, when standardized for size (geometric mean of all measured dimensions) and controlled for sex, only two of 10 differences were statistically significant, and for all but four of 20 comparisons (within sex) standardized measurement values were within 5%. The author concluded that while captivity may have some effect on articular surface morphology, because these effects are relatively minor and inconsistent, "there is no *a priori* reason to exclude captive individuals from morphological analyses" (p. 17).

The most extensive study of the effects of captivity on long bone diaphyseal structure in a great ape species was carried out by Morimoto et al. (2011). These authors examined cross-sectional geometries of captive and wild chimpanzees (*Pan troglodytes troglodytes*) at various levels of the femoral diaphysis and in three age groups (infants, older juveniles, and adults). They found no statistically significant differences in ontogenetic trajectories of the two groups, concluding that different loading conditions during growth do not alter genetically determined developmental programs. However, no information on length or timing of captivity, or the type of captive environment was available. In addition, femoral length was used as a proxy for age, which may be problematic given different rates of skeletal maturation between captive and wild chimpanzees (Zihlman et al., 2007), and analyses combined both static adult and

ontogenetic allometry. In a subsequent study, Morimoto et al. (2014) compared femoral diaphyseal morphology in four species/subspecies of *Pan* (most specimens in the study were wild). Phenotypic distances matched genotypic differences between taxa best in infancy, and then diverged. Although the authors interpreted this to reflect differences in "genetically determined taxon-specific developmental programs" (p. 6), an equally parsimonious explanation is that environmental, including locomotor, differences between taxa (Doran, 1992; Doran and Hunt, 1994) explain the different ontogenetic trajectories after infancy.

Except for Lewton (2017), a problem with all of these studies is that the history of many or all of the captive animals was not known, i.e., when they were captive and the conditions of captivity, especially the opportunities to practice realistic (wild-simulating) locomotor behavior. These details of an individual's history are critical, because the effects of altered mechanical loadings on bone structure vary during development (Pearson and Lieberman, 2004; Ruff et al., 1994), and because enclosure styles themselves have undergone extensive changes in an attempt to create more naturalistic environments (Kawata, 2011; Newberry, 1995; Ross et al., 2011; also, see SI Text). Just as great ape enclosures are different today than they were in the past, captive apes of the past may be behaviorally different than captive apes of the present – not all captivity should be considered equal. Also, with the exceptions of Morimoto et al.'s studies (2011, 2014) and a case study assessing the developmental stages of a single captive gorilla (Joganic, 2016), potential differentiation of morphology during growth and development within captive and wild environments has not been previously assessed. If environmental effects during growth are significant, then captive and wild infants of the same taxon should be more similar in morphology than their adult counterparts. Conversely, genetic effects between

taxa should be apparent in infancy. Thus, infants from the same taxon, whether captive or wild, should be more similar to each other than either is to infants of another taxon.

In this study we compare cross-sectional diaphyseal structure of the humerus, femur, and tibia between captive and wild infant/young juvenile and adult *Gorilla gorilla gorilla* (Western lowland gorillas). We define our captive sample as individuals either born in captivity or captured from the wild during infancy (see Materials and Methods for more details). In addition, we compare the same parameters with age-matched samples of wild Virunga *Gorilla beringei beringei* (Eastern mountain gorillas). Adult *G. b. beringei* are more terrestrial than adult *G. g. gorilla* (Doran, 1996, 1997; Doran-Sheehy et al., 2009; Knigge et al., 2015; Masi, 2004; Remis, 1995, 1998, 1999; Ruff et al., 2013, 2018; Schaller, 1963). Because opportunities for natural behavior in captive environments are generally more limited and can reflect substrate complexities (Ross et al., 2009; 2011), we predict that where adult wild *G. g. gorilla* and *G. b. beringei* differ in morphology, captive adult *G. g. gorilla* will more closely resemble the more terrestrial *G. b. beringei*. We also predict that, if there are differences between taxa, captive and wild *G. g. gorilla* will be more similar in infancy than either is to infant *G. b. beringei*, following the reasoning presented above. Locomotor behavior is also more similar in infant *G. g. gorilla* and *G. b. beringei* [Ruff et al., 2013, 2018]; therefore, structural differences are more likely to be a result of genetic effects.

The structural parameter on which we focus here is the (ln) ratio of anteroposterior (A-P) to mediolateral (M-L) bending strength. There are several reasons for concentrating on this particular characteristic: a) It avoids problems in accounting for possible differences in body size; b) it is known to change (in the femur) during ontogeny in both humans (Cowgill et al.,

2010) and chimpanzees (Morimoto et al., 2011); **c**) it has been shown to respond to differences in mechanical loading during growth (Carlson and Judex, 2007; MacDonald et al., 2009; Shaw and Stock, 2009a,b); **d**) it varies systematically between and within primate taxa, at least in part in relation to locomotor differences (Ruff, 1987, 1989; Ruff et al., 2015); **e**) mechanical interpretations of observed variation in the index are relatively straightforward.

Thus, our four hypotheses are: (1) adult gorillas raised in captivity will show different A-P/M-L diaphyseal bending strength ratios than their wild conspecifics; (2) any captive-wild shape differences among adults from the same taxon will not be significant early in ontogeny; (3) adult captive *G. g. gorilla* will be more similar in cross-sectional strength ratios to **wild** *G. b. beringei* than to wild *G. g. gorilla*; and (4) infant captive *G. g. gorilla* will be more similar in strength ratios to wild *G. g. gorilla* than to **wild** *G. b. beringei*.

MATERIALS AND METHODS

1. Sample

The sample included femora, tibiae, and humeri of six samples of gorillas – juvenile ($n = 4$) and adult ($n = 10$) captive *Gorilla gorilla gorilla*, juvenile ($n = 26$) and adult ($n = 36$) wild *G. g. gorilla*, and juvenile ($n = 24$) and adult ($n = 51$) wild *G. beringei beringei* (Tables 1 & 2; [see SI Table 1 for list of all specimens](#)). Captive specimens were obtained from collections curated by the Field Museum of Natural History (FMNH; Chicago, IL) and the National Museum of Natural History (NMNH; Washington, DC). All captive specimen information (including museum

provenance) is available in Supplementary Information ([SI Table 2](#)). Data for wild specimens were obtained from previous studies (Ruff et al., 2013, [2018](#)).

[Insert Table 1 Here]

1.1 *Captive G. g. gorilla Sample*

We were very selective in choosing our adult captive sample – including only those that could be identified by name and, subsequently, whose histories could be traced (Table 2; also see [SI Table 2](#)). Although this reduced our overall sample size, it creates a stronger argument for defining “captivity” (which we use here to define zoo animals, rather than laboratory or entertainment animals) in morphological studies. Therefore, our captive sample includes four adults who were born in captivity (between 1974–1990) at the Audubon Zoo (New Orleans, LA), Lincoln Park Zoo (LPZ; Chicago, IL), and Brookfield Zoo (BZ; Chicago, IL). The remaining six adults were born wild (between ~1947–1968) but were captured around one year of age (except for two individuals who were captured at around three and four years of age). Their first captive institutions following their capture were BZ, LPZ, and the Philadelphia Zoo ([PZ](#); Philadelphia, PA). Transfer information, enclosure settings, and cause of death (for some) are available in [SI Table 2](#) and additional information is given in SI Text. All adult specimens died between 13 and ~44 years of age at BZ, LPZ, or the National Zoological Park (NZIP; Washington, DC).

To minimize possible environmental effects of captivity on long bone morphology in our immature sample, [the sample](#) was restricted to individuals four years of age or younger, which

we refer to here as "infants." This sample was smaller than our adult sample, due to the limited availability of specimens in this age range. We obtained two individuals that died at approximately one year of age and two that died at approximately three and four years of age. Specimens had no obvious pathologies. One infant was identified as having been born captive at BZ and one was born wild and was taken to BZ at about one year of age. Histories for the other two specimens were unobtainable, though they died at LPZ.

[Insert Table 2 Here]

1.2 Wild Gorilla Samples

The comparative wild sample of western gorillas (*G. g. gorilla*) included 36 adults and 26 juveniles, while wild mountain gorillas (*G. b. beringei*) included 51 adults and 24 juveniles. The infant samples were limited to those at least three months and less than five years of age to best match with the captive specimen ages (see Table 1 and SI Fig. 1).

2. Measurements

2.1 Linear Measurements

Long bone lengths, used to identify cross section locations (length'), were determined for each specimen following Ruff (2002). All length' measurements were taken parallel to the longitudinal axis of the diaphysis on a customized osteometric board with a measurement wedge (see Ruff and Hayes, 1983: Fig. 3). For adult femora, length' was the distance from the

superior surface of neck to the average of the distal projections of the condyles; for adult tibiae, between the average longitudinal positions of the medial and lateral tibia plateaus and the center of the tibiotalar surface; and for adult humeri, from the most proximal point on the humeral head to the lateral lip of the trochlea. Maximum diaphyseal lengths, without epiphyses, were measured for the infant samples.

2.2 Cross-sectional Measurements

All captive specimens were scanned using peripheral quantitative computed tomography (pQCT). pQCT is a non-invasive high-resolution computed tomography technique that can be used to obtain bone structural properties (Ferretti et al. 1996; Schiessl et al., 1996). The scanner used here (Stratek SCT Research SA) has a maximum resolution (minimum pixel size) of 0.09 mm, which was utilized for the smallest infants, though larger specimens were scanned between 0.15–0.30 mm (Ruff et al., 2013) depending on the size of the specimen. Before scanning, each bone was placed in a standardized orientation, and diaphyseal scan locations marked (see Ruff, 2002).

Adult specimens were scanned at 50% of length for the tibia and femur and 40% of length from the distal end for the humerus (to avoid the deltoid tuberosity). Following previous analyses (Ruff et al., 2013), infant specimens were scanned at homologous locations of 45% (femur), 53% (tibia), and 41% (humerus) of diaphyseal length from the distal end.

Cross-sectional properties were automatically computed using the pQCT's built-in software. The properties examined here were Z_x (anteroposterior bending strength) and Z_y (mediolateral bending strength). As discussed above, the ratio of Z_x to Z_y describes cross-

sectional shape in terms of relative bending strength in different planes and has been shown to be biomechanically significant in a number of contexts (see Introduction).

3. Analysis

For comparisons between groups, the ratios of each bone's bending strength (Z_x/Z_y) were log-transformed (natural log; for justification, see Ruff, 2002). In two-way ANOVAs of bending strength ratios in adults, with sex and group (captive/wild *G. g. gorilla*, *G. b. beringei*) as factors, there were no significant sex-group interactions, and patterns of variation within sex were similar to those in pooled-sex analyses (sex-specific results are shown graphically in SI Figs. 2 & 3). Therefore, and to increase within-group sample sizes and statistical power (i.e., reduce Type II error), males and females were pooled for all analyses.

All data were tested for normality using Shapiro-Wilk tests. When data were normally distributed ($p > 0.05$), parametric tests were used – two-sample t-test comparisons between captive and wild *G. g. gorilla*, and ANOVA followed by pairwise post-hoc Tukey HSD tests for three-way comparisons between captive and wild *G. g. gorilla* and (wild) *G. b. beringei*. When data were not normally distributed, nonparametric Mann-Whitney U tests (two samples) or Kruskal-Wallis tests (three samples) followed by pairwise Mann-Whitney tests with Bonferroni correction were employed. A probability level of 0.05 (with Bonferroni correction, when used) was considered statistically significant.

In addition to comparisons of log ratios, we also present bivariate plots of log-transformed Z_x on Z_y for each section in the three samples (captive and wild *G. g. gorilla* and *G. b. beringei*). These allow for better visualization of individual variation and size-related trends.

Least squares regression lines were plotted through each sample, and ANCOVA used to assess inter-group differences in elevation. Correlations are uniformly quite high - $r > 0.94$ - so the method of line fitting makes little difference. All statistical analyses were performed using IBM SPSS Statistics version 24 and SYSTAT 13 for Macintosh.

RESULTS

We first present the results of comparisons between captive and wild *G. g. gorilla* adults and infants, followed by three-group comparisons including *G. b. beringei*. Shapiro-Wilk results from normality testing are available in supplementary information (SI Table 3) as are the log-transformed data for each specimen (SI Table 4).

[Insert Table 3 Here]

1. Captive versus wild *G. g. gorilla* adults

As predicted, captive and wild *G. g. gorilla* adults were significantly different in morphology in all three bones (Table 3, Fig. 1). Following normality testing (Shapiro-Wilk), (ln) femur Z_x/Z_y was examined with an Independent Samples t-test with pooled variance ($p = 0.005$; Levene's Test showed no significant difference in variance), while (ln) tibia Z_x/Z_y ($p = 0.009$) and (ln) humerus Z_x/Z_y ($p = 0.003$) were tested using Mann-Whitney U tests.

The lower Z_x/Z_y ratios of the wild *G. g. gorilla* hind limb bones (Fig. 1a,b) indicate relatively higher M-L bending strength (or lower A-P bending strength) compared with the

diaphyses of captive *G. g. gorilla* adults. Conversely, wild gorilla humeri (Fig. 1c) have relatively higher A-P bending strength than those of captive gorillas. These differences are also clearly shown in scatterplots of Z_x on Z_y (Fig. 2). Results of line elevation comparisons using ANCOVA are similar to those for comparisons of log ratios, with significant differences ($p < 0.02$) between wild and captive *G. g. gorilla* in all comparisons.

2. Captive versus wild *G. g. gorilla* infants

We predicted that cross-sectional morphology would not be statistically different between captive and wild *G. g. gorilla* immature individuals (“infants”). We found that indeed, there were no significant differences between the infant groups in any of the bones (Table 3, Fig. 3; $p > 0.20$). Although the samples were normally distributed (Shapiro-Wilk), there was a clear large discrepancy in sample sizes (captive: $n = 4$, wild: $n = 26$); therefore, nonparametric testing was used throughout (Mann-Whitney U tests). Overlap between captive and wild specimens is extensive for all comparisons, with particularly close matching of distributions for the hind limb bones (Fig. 3a,b; compare with adults in Fig. 1a,b). The very similar scaling of Z_x to Z_y in captive and wild infant *G. g. gorilla* for all sections is also apparent in scatterplots (Fig. 4). Line elevational differences were all nonsignificant ($p > 0.30$).

[Insert Table 4 Here]

3. *G. g. gorilla* versus *G. b. beringei* adults

We predicted that *if* differences existed between the cross-sectional diaphyseal shapes of adult *G. g. gorilla* and *G. b. beringei*, those differences would be found in the wild samples, while captive *G. g. gorilla* would more closely approximate the (more terrestrial) *G. b. beringei* distribution. This was found to be the case for the hind limb bones, but not for the humerus (Table 4, Fig. 1). To avoid redundancy with the results given above, in all reporting of three-group comparisons below, only the *G. g. gorilla* (wild and captive) versus *G. b. beringei* results are discussed; pairwise statistical results for captive vs. wild *G. g. gorilla* were similar to those provided earlier in the two-group comparisons.

Femoral Z_x/Z_y was the one variable that was normally distributed across all three groups and so was analyzed using a one-way ANOVA, which was significant ($p = 0.001$). This was followed by post-hoc Tukey HSD tests, demonstrating that wild *G. g. gorilla* was significantly different than *G. b. beringei* ($p = .019$), while captive *G. g. gorilla* was not ($p = 0.115$; Fig. 1a). As an additional check (due to very different sample sizes - see Table 1), nonparametric testing was also carried out, and gave equivalent results (Kruskal-Wallis: $p = 0.002$; Mann-Whitney U tests with Bonferroni correction ($\alpha = 0.016$): captive *G. g. gorilla* versus *G. b. beringei*, $p = 0.036$; wild *G. g. gorilla* versus *G. b. beringei*, $p = 0.006$).

For the tibia, wild *G. g. gorilla* and *G. b. beringei* were normally distributed but captive *G. g. gorilla* was not; therefore, nonparametric testing was used throughout. The three groups were found to vary significantly (Kruskal-Wallis: $p = 0.002$). Wild *G. g. gorilla* and *G. b. beringei* differed significantly (Mann-Whitney: $p = 0.003$), but captive *G. g. gorilla* and *G. b. beringei* did not (Mann-Whitney: $p = 0.206$; Fig. 1b).

For the humerus, all three groups were non-normal in their distribution, so were assessed non-parametrically and found to vary significantly (Kruskal-Wallis: $p < 0.001$). Applying Mann-Whitney U tests (with Bonferroni correction): wild *G. g. gorilla* and *G. b. beringei* were significantly different ($p = 0.004$) as were captive *G. g. gorilla* and *G. b. beringei* ($p < 0.001$; Fig. 1c).

Regressions of Z_x on Z_y (Fig. 2) demonstrate the same relationships, with significant differences in elevation for the femur and tibia between wild *G. g. gorilla* and *G. b. beringei* ($p < 0.02$) but not between captive *G. g. gorilla* and *G. b. beringei* ($p > 0.15$); while the humerus is nonsignificantly different in elevation between wild *G. g. gorilla* and *G. b. beringei* ($p = 0.20$) but significantly different in captive *G. g. gorilla* and *G. b. beringei* ($p = 0.001$).

[Insert Figure 1 Here]

[Insert Figure 2 Here]

4. *G. g. gorilla* versus *G. b. beringei* infants

Finally, we predicted that where differences in shape among infants existed, captive *G. g. gorilla* infants would be more similar in shape to wild *G. g. gorilla* infants than to *G. b. beringei* infants. As shown above, captive and wild *G. g. gorilla* infants were not significantly different from each other in any bone (Table 3, Fig. 3), so the potential contrast here was between taxa (Table 4). Individual ratios for infants are plotted in SI Figure 1.

As in the previous comparisons among infants, because of the disproportion in sample sizes (captive *G. g. gorilla* infants: $n = 4$; wild *G. g. gorilla* infants: $n = 26$; *G. b. beringei* infants: n

= 24), we chose to use nonparametric testing here. Based on initial Kruskal-Wallis tests, the tibia ($p = 0.815$) and humerus ($p = 0.470$) were not significantly different among the three groups. The femur, however, did vary significantly among the groups (Kruskal-Wallis: $p < 0.001$). Using Mann-Whitney U-tests with Bonferroni correction, wild *G. g. gorilla* infants had a significantly lower ratio than *G. b. beringei* infants ($p < .001$; Fig. 3a). Captive *G. g. gorilla* infants were very similar in distribution to wild *G. g. gorilla* and lower than *G. b. beringei*, but the difference from *G. b. beringei* did not quite reach statistical significance ($p = .030$) with Bonferroni correction ($\alpha = 0.016$). Scatterplots of Z_x on Z_y (Fig. 4) also clearly demonstrate these patterns, with wild and captive *G. g. gorilla* infants grouping closely for the femur ($p = 0.96$, elevation test) and each significantly different in elevation from *G. b. beringei* ($p < 0.005$). For the tibia and humerus, all three groups are very similar in distribution ($p > 0.60$, elevation tests).

[Insert Figure 3 Here]

[Insert Figure 4 Here]

DISCUSSION

Our results support our primary hypotheses regarding the biomechanically relevant effects of captivity on the morphology of *Gorilla gorilla gorilla* postcrania (humerus, femur, and tibia). Diaphyseal cross-sectional morphology in captive and wild *G. g. gorilla* was similar among infants, but diverged in adults in all three bones. Our secondary hypotheses regarding

similarities or differences between *G. g. gorilla* and *G. beringei beringei* were also largely borne out. Where differences in morphology existed between adults, captive *G. g. gorilla* was more similar to the more terrestrial *G. b. beringei* in the hind limb bones. In contrast, all infants were generally more similar in morphology, but where they differed – in the femur – captive and wild *G. g. gorilla* were more similar to each other than either was to *G. b. beringei*. The only exception to our predictions was in comparisons of humeral morphology among adults in the three groups, where both captive and wild *G. g. gorilla* were different from *G. b. beringei*.

Our results differ from those of Morimoto et al. (2011), who argued for the primacy of genetically determined developmental trajectories in producing adult diaphyseal morphology in chimpanzees. In contrast, our results strongly favor environmental effects on long bone cross-sectional geometry during growth in response to captivity. Not only did captive and wild *G. g. gorilla* diverge in morphology between infancy and adulthood, but either captive or wild adult *G. g. gorilla* were more similar in morphology to *G. b. beringei* than they were to each other, contrary to predictions if phylogeny were the primary driver of morphological differentiation. This does not mean that genetic influences are not potentially significant - the difference in femoral cross-sectional morphology between both captive and wild *G. g. gorilla* and *G. b. beringei* infants may be such an example. However, our results are most consistent with environmental modification of developmental trajectories for long bone cross-sectional morphology in gorillas (also see Ruff et al., 2013, 2018). It should be noted that our study evaluated *Gorilla* while Morimoto et al. (2011) measured *Pan* – leaving the possibility of genus-level differences. Lewton (2017) found only a few differences in the articular morphologies of captive and wild chimpanzees; however, articulations appear to be more genetically canalized

during growth than cross-sectional diaphyseal dimensions (Auerbach and Ruff, 2007; Lieberman et al., 2001; Reeves et al., 2016; Trinkaus et al., 1994). Other studies have shown developmental changes in limb bone diaphyseal proportions among wild chimpanzees related to changes in locomotor behavior (Sarringhaus et al., 2016). Additional studies on better-defined captive groups are needed to evaluate the effects of captivity *per se* on long bone structural differences in chimpanzees as well as other primate taxa.

Limb bone loadings during locomotion in gorillas

We found that adult captive *G. g. gorilla* has relatively lower M-L bending strength of the femur and tibia than wild *G. g. gorilla*. These differences were not present among infant *G. g. gorilla*, so we attribute them to the captive environment. Because bending strength ratios reflect mechanical loadings in specific planes, and not, for example, overall bone size, they are unlikely to be caused by general systemic effects on the skeleton such as diet, but rather to specific behavioral modifications (Carlson and Judex, 2007; MacDonald et al., 2009; Shaw and Stock, 2009a,b). One result of a non-naturalistic (see Kawata, 2011 and SI Text) zoo environment on large-bodied hominoids is a relative lack of opportunities for locomotion on arboreal substrates, including climbing. The fact that adult captive *G. g. gorilla* more closely resemble adult *G. b. beringei*, who are more terrestrial than wild *G. g. gorilla* (Doran, 1997; Ruff et al., 2018), also suggests that the critical behavioral modification among captives may be related to lower frequencies of arboreality.

[Insert Figure 5 Here]

Many investigators have stressed the importance of foot inversion (and dorsiflexion) during vertical climbing in nonhuman hominoids (DeSilva, 2009; Holowka et al., 2017; Wunderlich and Ischinger, 2017; and see Fig. 4b). Anatomical correlates of this behavior have been documented in the talus of *G. g. gorilla* compared to that of *G. b. beringei*, which is better adapted for more sagittally-constrained terrestrial loadings (Dunn et al., 2014; Knigge et al., 2015). Foot inversion during climbing is combined with knee flexion and hip abduction and flexion, which displaces the knee laterally (Fig. 4b; Isler, 2005; Neufuss et al., 2017). This would be expected to increase M-L bending loads on the hind limb bones relative to those engendered by the more parasagittal movements characteristic of terrestrial quadrupedalism (i.e., knuckle-walking). Because of the lack of appropriate substrates (i.e., large vertical supports), even when captive gorillas climb, they may not be able to climb in the same manner as wild gorillas, instead again using more parasagittal positioning of the hind limbs (Fig. 4a). Thus, relatively decreased M-L bending strength of the femur and tibia in captive gorillas (and wild mountain gorillas) may be related to lower frequencies of naturalistic vertical climbing behavior. This is also consistent with observed differences in ankle morphology between captive and wild gorillas (Venkataraman et al., 2013).

Our results for the humerus are more difficult to interpret in an explicitly mechanical context. Again, captive and wild *G. g. gorilla* diverged in morphology after infancy, but in this case the wild adults more closely resembled *G. b. beringei* in having higher A-P/M-L strength indices. Vertical climbing in naturalistic environments does result in characteristic forelimb positioning (Fig. 4b), although the specific degrees of elbow flexion and shoulder elevation are

strongly dependent on substrate size in gorillas (Neufuss et al., 2017), which could affect A-P versus M-L loadings. Vertical climbing in captive gorillas may differ systematically in terms of forelimb positioning (Fig. 4), but the specific effects on forelimb loads are more difficult to predict. The forelimb is also more of a “multifunctional” organ, involved in frequent non-locomotor behavior (e.g., manipulation). Inclusion of the distal forelimb long bones – the radius and ulna – might also reveal differences related to captivity, since variation in apparent load-sharing between these have been observed among wild gorillas, possibly due to relatively subtle differences in hand positioning during locomotion (Ruff et al., 2013, 2018).

Study limitations

The small number of captive infants, combined with some heterogeneity in structural proportions in this age group (SI Fig. 1), may have worked against detection of differences between the samples. However, the four captive infant specimens that were available span an important age range in development, including two individuals who died early in infancy and two who died somewhat later, so are representative of early development overall – including slight age trends during this period of growth (SI Fig. 1). The captive specimens also span a size range similar to that of the other two infant samples (Fig. 4). Additional captive specimens spanning the entire spectrum of infancy and juvenility will create a more complete picture of when cross-sectional morphology begins to diverge between captive and wild individuals. Our sample of captive adults was larger (n = 10), and importantly, all but two (“Otto” and “Haloko”) had been captive since about one year of age. The removal of the eldest when captured, “Otto” (aged four when captured), from our sample does not affect our findings.

Another limitation is that we do not have records of actual behaviors of our captive study sample, so must infer these from qualitative assessments based on photographs, newspaper articles, and video footage (see SI Text). Quantitative behavioral studies could be useful in this regard, although given the changes in zoo practices over the past few decades (summarized in SI Text), it is unlikely that results would be representative of the conditions prevalent at the time that our study sample was captive. Expansion of the sample to include individuals from a wider range of captive environments, including more recent environments, would also be an interesting extension of the present study (see SI Text and [SI Table 2](#)). In this sense, long bone morphology could serve as an additional test of the efficacy of these changes in establishing more naturalistic conditions.

CONCLUSIONS

We present the first study investigating differences in long bone diaphyseal structure between captive and wild western lowland gorillas (*Gorilla gorilla gorilla*). We predicted that dissimilarities in femoral, tibial, and humeral morphology between the two groups would reflect environmental differences – as postcranial diaphyseal morphology has been shown to reflect dynamic loadings during growth. We found that captive and wild *G. g. gorilla* did in fact change in long bone diaphyseal shape during development, beginning in infancy with very similar morphologies but diverging by adulthood. We also compared our *G. g. gorilla* samples to age-matched individuals of Virunga mountain gorillas (*G. beringei beringei*) because of their high degree of terrestriality. Where there were differences between wild *G. g. gorilla* and *G. b.*

beringei adults, captive adults most closely resembled *G. b. beringei* in the hind limb. Based on these comparisons and behavioral observations on hind limb positioning during locomotion, we hypothesize that the differences in hind limb morphology between captive and wild *G. g. gorilla* are due to less vertical climbing among the captive animals (as well as *G. b. beringei*). Morphological differences related to phylogeny were most evident early in development where captive and wild *G. g. gorilla* infants did not differ from each other, while there were differences between *G. g. gorilla* and *G. b. beringei*.

ACKNOWLEDGEMENTS

We are grateful to Lawrence Heaney (Field Museum of Natural History) and to Darrin Lunde and David Hunt (National Museum of Natural History, Smithsonian Institution) for access to the captive specimens. Funding for collection of the comparative dataset was provided by the National Science Foundation (BCS-1316104, BCS-1419564), the L.S.B. Leakey Foundation, the Wenner-Gren Foundation for Anthropological Research (8657), and the University of Oulu, Finland. Access to the mountain gorilla comparative sample was provided by Shannon McFarlin (The George Washington University) and the Mountain Gorilla Skeletal Project, supported by the National Science Foundation (BCS-0852866, BCS-0964944), National Geographic Society's Committee for Research and Exploration (8486-08), the L.S.B. Leakey Foundation, the Rwanda Development Board's Department of Tourism and Conservation, Dian Fossey Gorilla Fund International's Karisoke Research Center, Gorilla Doctors, and The George Washington

University. Finally, we are grateful to two anonymous reviewers and the Associate Editor for their helpful comments for revising this manuscript.

AUTHOR CONTRIBUTIONS: S.L. Canington and C.B. Ruff conceived and designed the study; S.L. Canington and A.D. Sylvester acquired the captive data; C.B. Ruff, M.L. Burgess, and J-A. Junno provided the previously collected comparative data; S.L. Canington, A.D. Sylvester, and C.B. Ruff carried out analyses and prepared the figures; S.L. Canington and C.B. Ruff wrote the paper; and A.D. Sylvester provided critical comments on the paper.

REFERENCES

- Auerbach, B. M., & Ruff, C. B. (2006). Limb bone bilateral asymmetry: Variability and commonality among modern humans. *Journal of Human Evolution*, 50, 203–218.
- Bello-Hellegouarch, G., Potau, J. M., Arias-Martorell, J., Pastor, J. F., & Pérez-Pérez, A. (2013). Brief communication: Morphological effects of captivity: A geometric morphometric analysis of the dorsal side of the scapula in captive-bred and wild-caught hominoidea. *American Journal of Physical Anthropology*, 152, 306–310.
- Berkovich, H. (rgbstock) <http://www.rgbstock.com/photo/mC07Qd6/gorilla>.
- Biewener, A. A., & Bertram, J. E. (1994). Structural response of growing bone to exercise and disuse. *Journal of Applied Physiology*, 76, 946–955.
- Boorer, M. K. (1972). Some aspects of stereotyped patterns of movement exhibited by zoo animals. *International Zoo Yearbook*, 12, 164–168.

- Canington, S. L., & Hunt, D. R. (2016). Rapid development of secondary hyperparathyroidism and fibrous osteodystrophy in a juvenile orangutan. *International Journal of Paleopathology*, 13, 96–99.
- Carlson, K. J., & Judex, S. (2007). Increased non-linear locomotion alters diaphyseal bone shape. *Journal of Experimental Biology*, 210, 3117–3125.
- Clarke, A. S., Juno, C. J., & Maple, T. L. (1982). Behavioral effects of a change in the physical environment: a pilot study of captive chimpanzees. *Zoo Biology*, 1, 371–380.
- Cousins, D. (1972). Diseases and injuries in wild and captive gorillas: *Gorilla gorilla*. *International Zoo Yearbook*, 12, 211–218.
- Cowgill, L. W., Warrener, A., Pontzer, H., & Ocobock, C. (2010). Waddling and toddling: The biomechanical effects of an immature gait. *American Journal of Physical Anthropology*, 143, 52–61.
- DeSilva, J. M. (2009). Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proceedings of the National Academy of Sciences*, 106, 6567–6572.
- Doran, D. M. (1992). The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. *Journal of Human Evolution*, 23, 139–157.
- Doran, D. M. (1996). Comparative positional behavior of the African apes. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 213–224). Cambridge: Cambridge University Press.
- Doran, D. M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, 32, 323–344.

- Doran, D. M., & Hunt, K. D. (1994). Comparative locomotor behavior of chimpanzees and bonobos: species and habitat differences. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 93–106). Cambridge, MA: Harvard University Press.
- Doran-Sheehy, D., Andrianady, M., & Lodwick, J. (2009). Sex differences in western gorilla arboreality. *American Journal of Physical Anthropology Suppl.*, 48, 120.
- Dunn, R. H., Tocheri, M. W., Orr, C. M., & Jungers, W. L. (2014). Ecological divergence and talar morphology in gorillas. *American Journal of Physical Anthropology*, 153, 526–541.
- Farrell, M., Rando, C., & Garrod, B. (2015). Lessons from the past: Metabolic bone disease in historical captive primates. *International Journal of Primatology*, 36, 398–411.
- Ferretti, J. L., Capozza, R. F., & Zanchetta, J. R. (1996). Mechanical validation of a tomographic (pQCT) index for noninvasive estimation of rat femur bending strength. *Bone*, 18, 97–102.
- Films Incorporated (1978). Wilmette, IL. <https://archive.org/details/ottozoogorilla>, reel01-02, 0:22.
- Fleagle, J. G., & Meldrum, D. J. (1988). Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *American Journal of Primatology*, 16, 227–249.
- Garn, S. M., Guzmán, M. A., & Wagner, B. (1969). Subperiosteal gain and endosteal loss in protein-calorie malnutrition. *American Journal of Physical Anthropology*, 30, 153–155.
- Green, D. J., Richmond, B. G., & Miran, S. L. (2012). Mouse shoulder morphology responds to locomotor activity and the kinematic differences of climbing and running. *Journal of*

- Experimental Zoology Part B: Molecular and Developmental Evolution*, 318, 621–638.
- Holowka, N. B., O'Neill, M. C., Thompson, N. E., & Demes, B. (2017). Chimpanzee ankle and foot joint kinematics: Arboreal versus terrestrial locomotion. *American Journal of Physical Anthropology*, 164, 131–147.
- Isler, K. (2005). 3D - Kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology*, 126, 66–81.
- Joganic, J. L. (2016). Skeletal and dental development in a sub - adult western lowland gorilla (*Gorilla gorilla gorilla*). *American Journal of Physical Anthropology*, 159, 174–181.
- Jones, H. H., Priest, J. D., Hayes, W. C., Tichenor, C. C., & Nagel, D. A. (1977). Humeral hypertrophy in response to exercise. *Journal of Bone and Joint Surgery Am.*, 59, 204–208.
- Kawata, K. (2011). Romancing the celluloid nature: A review of American zoo exhibits, part I. *Der Zoologische Garten*, 80, 239–253.
- Kelley, J.L., & Garcia, C.M. (2010). Ontogenetic effects of captive breeding. In M. D. Breed, & J. Moore (Eds.), *Encyclopedia of Animal Behavior* (pp. 589–595). Oxford: Academic Press.
- Knigge, R. P., Tocheri, M. W., Orr, C. M., & McNulty, K. P. (2015). Three - dimensional geometric morphometric analysis of talar morphology in extant gorilla taxa from highland and lowland habitats. *The Anatomical Record*, 298, 277–290.
- Lee, K. C. L., Maxwell, A., & Lanyon, L. E. (2002). Validation of a technique for studying functional adaptation of the mouse ulna in response to mechanical loading. *Bone*, 31, 407–412.
- Less, E. H., Kuhar, C. W., Dennis, P. M., & Lukas, K. E. (2012). Assessing inactivity in zoo gorillas

- using keeper ratings and behavioral data. *Applied Animal Behaviour Science*, 137, 74–79.
- Lewton, K. L. (2017). The effects of captive versus wild rearing environments on long bone articular surfaces in common chimpanzees (*Pan troglodytes*). *PeerJ*, 5, e3668.
- Lieberman, D. E., Devlin, M. J., & Pearson, O. M. (2001). Articular area responses to mechanical loading: effects of exercise, age, and skeletal location. *American Journal of Physical Anthropology*, 116, 266–277.
- MacDonald, H. M., Cooper, D. M. L., & McKay, H. A. (2009). Anterior–posterior bending strength at the tibial shaft increases with physical activity in boys: Evidence for non-uniform geometric adaptation. *Osteoporosis International*, 20, 61–70.
- Masi, S. (2004). Tree use by a western gorilla group (*Gorilla gorilla gorilla*) in the Dzanga-Ndoki National park, Central African Republic. *Folia Primatologica*, 75, 385–414.
- Morimoto, N., De León, M. S. P., & Zollikofer, C. P. E. (2011). Exploring femoral diaphyseal shape variation in wild and captive chimpanzees by means of morphometric mapping: A test of Wolff's Law. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, 294, 589–609.
- Morimoto, N., León, M. S. P. de, & Zollikofer, C. P. E. (2014). Phenotypic variation in infants, not adults, reflects genotypic variation among chimpanzees and bonobos. *PLOS ONE*, 9, e102074.
- Neufuss, J., Robbins, M. M., Baeumer, J., Humle, T., & Kivell, T. L. (2017). Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 164, 651–664.

- Newberry, R. C. (1995). Environmental enrichment: Increasing the biological relevance of captive environments. *Applied Animal Behaviour Science*, 44, 229–243.
- O'Connor, J. A., Lanyon, L. E., & MacFie, H. (1982). The influence of strain rate on adaptive bone remodelling. *Journal of Biomechanics*, 15, 767–781.
- O'regan, H. J., & Kitchener, A. C. (2005). The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*, 35, 215–230.
- Pearson, O. M., & Lieberman, D. E. (2004). The aging of Wolff's "law": Ontogeny and responses to mechanical loading in cortical bone. *American Journal of Physical Anthropology*, 125, 63–99.
- Reeves, N. M., Auerbach, B. M., & Sylvester, A. D. (2016). Fluctuating and directional asymmetry in the long bones of captive cotton - top tamarins (*Saguinus oedipus*). *American Journal of Physical Anthropology*, 160, 41–51.
- Remis, M. (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*, 97, 413–433.
- Remis, M. J. (1998). The gorilla paradox. In E. Strasser, J. G. Fleagle, A. L. Rosenberger, & H. M. McHenry (Eds.), *Primate Locomotion* (pp. 95–106). New York: Springer Publishing.
- Remis, M. J. (1999). Tree structure and sex differences in arboreality among western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Primates*, 40, 383–396.
- Ross, S. R., Schapiro, S. J., Hau, J., & Lukas, K. E. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour*

Science, 121, 42–50.

- Ross, S. R., Wagner, K. E., Schapiro, S. J., Hau, J., & Lukas, K. E. (2011). Transfer and acclimatization effects on the behavior of two species of African great ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) moved to a novel and naturalistic zoo environment. *International Journal of Primatology*, 32, 99–117.
- Ruff, C. (1987). Sexual dimorphism in human lower limb bone structure: Relationship to subsistence strategy and sexual division of labor. *Journal of Human Evolution*, 16, 391–416.
- Ruff, C. B. (1989). New approaches to structural evolution of limb bones in primates. *Folia Primatologica*, 53, 142–159.
- Ruff, C. B. (2002). Long bone articular and diaphyseal structure in old world monkeys and apes. I: Locomotor effects. *American Journal of Physical Anthropology*, 119, 305–342.
- Ruff, C. B. (2003). Ontogenetic adaptation to bipedalism: Age changes in femoral to humeral length and strength proportions in humans, with a comparison to baboons. *Journal of Human Evolution*, 45, 317–349.
- Ruff, C. B. (2007). Biomechanical analyses of archaeological human skeletons. In M. A. Katzenberg & S. R. Saunders (Eds.), *Biological Anthropology of the Human Skeleton, Second Edition* (pp. 183–206). New Jersey: John Wiley & Sons, Inc.
- Ruff, C. B., Burgess, M. L., Bromage, T. G., Mudakikwa, A., & McFarlin, S. C. (2013). Ontogenetic changes in limb bone structural proportions in mountain gorillas (*Gorilla beringei beringei*). *Journal of Human Evolution*, 65, 693–703.
- Ruff, C. B., Burgess, M. L., Junno, J.-A., Mudakikwa, A., Zollikofer, C. P. E., Ponce de Leon, M. S.,

- & McFarlin, S. C. (2018). Phylogenetic and environmental effects on limb bone structure in gorillas. *American Journal of Physical Anthropology*, 166, 353–372.
- Ruff C. B., & Hayes W. C. (1983). Cross-sectional geometry of Pecos Pueblo femora and tibiae - a biomechanical investigation. I. Method and general patterns of variation. *American Journal of Physical Anthropology*, 60, 359–381.
- Ruff, C. B., Holt, B., Niskanen, M., Sladek, V., Berner, M., Garofalo, E., ... Whittey, E. (2015). Gradual decline in mobility with the adoption of food production in Europe. *Proceedings of the National Academy of Sciences*, 112, 7147–7152.
- Ruff, C., Holt, B., & Trinkaus, E. (2006). Who's afraid of the big bad Wolff?: "Wolff's law" and bone functional adaptation. *American Journal of Physical Anthropology*, 129, 484–498.
- Ruff, C. B., Walker, A., & Trinkaus, E. (1994). Postcranial robusticity in Homo. III: Ontogeny. *American Journal of Physical Anthropology*, 93, 35–54.
- Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2016). Long bone cross-sectional properties reflect changes in locomotor behavior in developing chimpanzees. *American Journal of Physical Anthropology*, 160, 16–29.
- Schaller, G. B. (1963). *The Mountain Gorilla: Ecology and Behavior*. Chicago and London: The University of Chicago Press.
- Schiessl, H., Ferretti, J. L., Tysarczyk-Niemeyer, G., & Willnecker, J. (1996). Noninvasive bone strength index as analyzed by peripheral quantitative computed tomography (pQCT). In E. Schönau (Ed.), *Paediatric Osteology: New Developments in Diagnostics and Therapy* (pp. 141–146). Amsterdam: Elsevier.
- Shaw, C. N., & Stock, J. T. (2009a). Habitual throwing and swimming correspond with upper

- limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*, 140, 160–172.
- Shaw, C. N., & Stock, J. T. (2009b). Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *American Journal of Physical Anthropology*, 140, 149–159.
- Strong, V. J., Grindlay, D., Redrobe, S., Cobb, M., & White, K. (2016). A systematic review of the literature relating to captive great ape morbidity and mortality. *Journal of Zoo and Wildlife Medicine*, 47, 697–710.
- Sutton, J. B. (1884). Observations on rickets in captive and wild animals. *Journal of Anatomy*, 18, 363–387.
- Trinkaus, E., Churchill, S. E., & Ruff, C. B. (1994). Postcranial robusticity in *Homo*. II: Humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology*, 93, 1–34.
- Venkataraman, V. V., Kraft, T. S., Desilva, J. M., & Dominy, N. J. (2013). Phenotypic plasticity of climbing-related traits in the ankle joint of great apes and rainforest hunter-gatherers. *Human Biology*, 85, 309–328.
- Vereecke, E. E., D’Août, K., & Aerts, P. (2011). Studying captive ape locomotion: Past, present, and future. In D’Août, K. & Vereecke, E. E. (Eds.), *Primate Locomotion* (pp. 29–46). New York: Springer.
- Wunderlich, R. E., & Ischinger, S. B. (2017). Foot use during vertical climbing in chimpanzees (*Pan troglodytes*). *Journal of Human Evolution*, 109, 1–10.
- 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, 63–73.

Figure Legends

Figure 1. Box plots of A-P/M-L bending strengths in adult captive and wild *G. g. gorilla*, and *G. b. beringei*: a) femur, b) tibia, c) humerus. See Table 1 for sample sizes, and Tables 3 and 4 for statistical comparisons between groups.

Figure 2. Scatterplots of A-P versus M-L bending strength in adult captive (red triangles) and wild (green circles) *G. g. gorilla*, and *G. b. beringei* (blue squares): a) femur, b) tibia, c) humerus. Least squares regression lines fit through each group.

Figure 3. Box plots of A-P/M-L bending strengths in infant captive and wild *G. g. gorilla*, and *G. b. beringei*: a) femur, b) tibia, c) humerus. See Table 1 for sample sizes, and Tables 3 and 4 for statistical comparisons between groups.

Figure 4. Scatterplots of A-P versus M-L bending strength in infant captive (red triangles) and wild (green circles) *G. g. gorilla*, and *G. b. beringei* (blue squares): a) femur, b) tibia, c) humerus. Least squares regression lines fit through each group.

Figure 5. Vertical climbing behaviors and body position given different substrates: a) Adult male in early enclosure style employs a parasagittal posture in both hind and forelimb (Films

Incorporated, 1978). b) Climbing posture typical of wild gorillas (Hagit Berkovich [rgbstock]). Note here the inverted foot, flexed knee, and abducted and flexed hip.