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Skeletal ageing in Virunga mountain gorillas

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Bone loss and heightened fracture risk are common conditions associated with ageing in modern human populations and have been attributed to both hormonal and other metabolic and behavioural changes. To what extent these age-related trends are specific to modern humans or generally characteristic of natural populations of other taxa is not clear. In this study, we use computed tomography to examine age changes in long bone and vertebral structural properties of 34 wild-adult Virunga mountain gorillas (*Gorilla beringei beringei*) whose skeletons were recovered from natural accumulations. Chronological ages were known or estimated from sample-specific dental wear formulae and ranged between 11 and 43 years. Gorillas show some of the same characteristics of skeletal ageing as modern humans, including endosteal and some periosteal expansion. However, unlike in humans, there is no decline in cortical or trabecular bone density, or in combined geometric-density measures of strength, nor do females show accelerated bone loss later in life. We attribute these differences to the lack of an extended post-reproductive period in gorillas, which provides protection against bone resorption. Increases in age-related fractures (osteoporosis) in modern humans may be a combined effect of an extended lifespan and lower activity levels earlier in life.

This article is part of the theme issue 'Evolution of the primate ageing process'.

1. Introduction

Bone loss and remodelling with ageing are well-documented phenomena in modern human populations [1–6]. In long bone diaphyses, endosteal expansion, partially offset by subperiosteal expansion, leads to cortical thinning, while trabecular bone apparent (bulk) density decreases in epiphyseal regions and vertebrae. There is also some decline in compact bone density. These trends begin by the fourth or fifth decade of life for compact cortical bone and in the third or fourth decade for trabecular bone, and progress more rapidly in post-menopausal females (see the electronic supplementary material, figures S1 and S2). Bone loss with ageing leads to increased risk of fracture, particularly in the hip and vertebral regions, with a higher risk in females and in modern industrial populations [7,8].

These age patterns and the difference between the sexes have been related to two underlying physiological mechanisms, referred to as Type I (Post-menopausal) and Type II (Senile) Osteoporosis [7]. Type I Osteoporosis, usually present only among females, is caused by a sharp reduction in estrogen levels following menopause, resulting in relatively rapid bone loss due to the

restraining effects of estrogen on bone resorption and its positive effects on bone formation [9]. Type II Osteoporosis is a more gradual cumulative process characteristic of both sexes that occurs throughout adulthood and may be attributed to reduced calcium absorption due to impaired production of vitamin D, among other factors [1]. The combined result of the two phenomena results in the observed rapid loss of bone among middle-aged females superimposed on more gradual losses in both sexes.

How these observations relate to broader evolutionary trends within hominins, including the evolution of an increased lifespan, a longer post-reproductive period, changes in lifestyle (especially activity level) and changes in diet, have been the subject of much discussion [10–14]. Comparisons of humans with our closest phylogenetic relatives—nonhuman primates—may shed light on the evolutionary timing and significance of these patterns.

Skeletal ageing in nonhuman primates has been examined by a number of investigators (for reviews, see [15–17]), most often in Old World monkeys, primarily macaques (e.g. [18–22]). Many of these investigations have demonstrated some age-related declines in bone mineral density (BMD) or relative cortical thickness that in some ways parallel those observed in humans. A potential limitation of most such studies is that they have been conducted on captive animals, where dietary supplementation as well as non-natural locomotor behaviour may affect patterns of skeletal ageing relative to those of wild populations [20,23,24]. Even in studies of macaques in more naturalistic environments [19,22], subjects were provisioned on commercial diets and had reduced home ranges compared to wild conspecifics [25].

Similar ageing studies of great apes have been much more limited. Several reports of skeletal age changes in wild chimpanzees (*Pan troglodytes schweinfurthii*) from Gombe, Tanzania have been presented [26–28]. Sample sizes were small (4–6 adult females, 2–5 adult males) and age estimates were approximate (to within about ±5 years) [27]. Old females had reduced diaphyseal bone mineral content (BMC), bone mineral index (BMC/bone width) and per cent cortical area. A study of BMD of the femoral neck and lumbar vertebrae of four *P. t. schweinfurthii* skeletons from Mahale, Tanzania showed much-reduced values in one old female [29]. A preliminary study of museum specimens aged qualitatively from dental wear found only slight age-related changes among chimpanzees and gorillas in trabecular density measured at several skeletal locations and cross-sectional geometric properties of the femur and humerus, although some medullary and periosteal expansion were noted among gorillas [30]. This is one of the only studies of skeletal ageing in nonhuman primates (also see [31]) that included geometric estimates of bone strength. Another limitation of almost all previous studies of bone density changes with ageing in nonhuman primates is that they have included only non-volumetric BMD measures, i.e. bone BMC divided by either bone width or two-dimensional area rather than volume, thus precluding estimates of true volumetric density (although see [21] for an exception).

In this study, we report the results of our analyses of 34 wild-adult Virunga mountain gorilla (*Gorilla beringei beringei*) skeletons with known ages or ages estimated using within-population dental wear or developmental standards. Age trends in diaphyseal cross-sectional geometric properties and volumetric bone mineral density (vBMD) of all of the major long bones are assessed. We also evaluate age-related
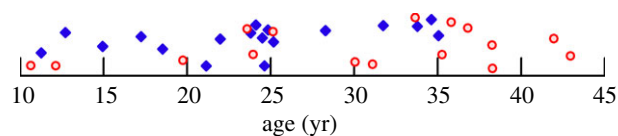
Figure 1. Age distribution of the Virunga sample. Red circles: females; blue diamonds: males. (Online version in colour.)

changes in lumbar vBMD in 21 individuals. These data are used to address the following questions: (i) Do wild mountain gorillas show patterns of bone loss and remodelling with age that are similar to those of humans? (ii) Are the sex differences in these patterns observed in humans also characteristic of gorillas? (iii) How do these results inform our understanding of the biological mechanisms underlying skeletal ageing in gorillas, and the evolution of the modern human pattern of skeletal ageing?

2. Material and methods

(a) Study sample
All specimens were obtained from collections of the mountain gorilla skeletal project (MGSP), a multidisciplinary collaboration to assist the Rwanda Development Board's Department of Tourism and Conservation (RDB) in the recovery and preservation of skeletal remains from deceased gorillas from Volcanoes National Park in Rwanda [32]. Most individuals in the collection were members of habituated groups monitored in life by RDB or Dian Fossey Gorilla Fund International's Karisoke Research Center; health monitoring and postmortem examinations following their natural deaths were conducted by Gorilla Doctors.

Sixteen females and 17 males were included in long bone structural analyses. All individuals had fully erupted third molars. Sexes for all individuals and ages for 23 individuals were known to the exact day or month from records of the Rwanda Development Board and Dian Fossey Gorilla Fund International's Karisoke Research Center (Musanze, Rwanda). In three cases, uncertainty in birth date (and thus age) ranged between ±1.5 and ±4 years (see electronic supplementary material, table S1 for details). Ages for 10 other individuals were estimated from incisor tooth wear using population-specific formulae developed for the MGSP sample [33] and for one individual from dental developmental maturity [34]. One additional individual was included in lumbar vertebral but not long bone analyses; its age was estimated from tooth wear [33]. Age distributions by sex are shown in figure 1. Known or estimated ages ranged from 10.7 to 43.0 years. The lower end of this range corresponds to the age of sexual maturity and attainment of greater than 92–95% of the final adult body or arm length in females [35], while the upper end is at the maximum lifespan observed for Virunga mountain gorillas [17,36].

(b) Bone structural properties
Bone structural data were obtained using peripheral quantitative computed tomography (pQCT) [37] (Stratec XCT Research SA or SA+, 50 kVp, 13–45 mAs). The manufacturer's phantom was scanned prior to each session to establish calibration factors. After orientation in standardized anatomical planes [38], sections perpendicular to the long axis of the diaphysis were scanned at 50% of length' (interarticular length—see [38]) in the femur, tibia, radius and ulna, and 40% of length' from the distal end in the humerus (to avoid the deltoid tuberosity). L3 lumbar vertebrae were scanned through the vertebral body in a coronal plane, at the anteroposterior midpoint of the body. Scan resolutions ranged from 0.20 to 0.30 mm (0.35 mm for vertebrae), and slice thickness was a constant 1.0 mm. A bone-air threshold of

Table 1. Age changes in bone structural properties.

property[a]	element	females			males		
		r	p	slope	r	p	slope
TA	femur	0.592	0.016	3.95	0.258	n.s.	
	tibia	0.573	0.020	2.05	0.318	n.s.	
	humerus		n.s.			n.s.	
	radius		n.s.		0.535	0.027	1.33
	ulna		n.s.			n.s.	
MA	femur	0.654	0.006	2.72	0.619	0.008	4.06
	tibia	0.697	0.003	1.43	0.476	0.053	1.45
	humerus		n.s.			n.s.	
	radius	0.535	0.027	0.85	0.556	0.020	1.33
	ulna[b]	0.754	0.002		0.597	0.018	
CA	all		n.s.			n.s.	
Z_p	femur	0.517	0.040	27.0		n.s.	
	tibia	0.522	0.038	10.7		n.s.	
	humerus		n.s			n.s.	
	radius		n.s.			n.s.	
	ulna		n.s			n.s	
	fem/hum[c]	0.758	0.001	0.006		n.s.	
SSI_p	all		n.s.			n.s.	
Cort. vBMD	all		n.s			n.s.	
Trab. vBMD	L3		n.s.			n.s.	

[a]TA, subperiosteal area; MA, medullary area; CA, cortical area; Z_p, polar section modulus; SSI, strength-strain index. Areas in mm^2, Z_p and SSI_p in mm^3. Cort., cortical; Trab., trabecular; vBMD, volumetric bone mineral density (g/cm^3).
[b]Quadratic fit. R is adjusted for multiple predictor variables. Regression coefficients: females: 2.26 (age), 0.10 (age^2); males: 1.70 (age), 0.16 (age^2).
[c]Ln(femur Z_p/humerus Z_p).

500 mg cm^{-3} was used for diaphyseal sections [39]. For vertebrae, a bone-air threshold of 0 mg cm^{-3} was used. Peripheral osteophytes and regions of periarticular sclerotic bone were manually trimmed. Trabecular bone was then isolated using the pQCT 'Concentric Peel' method to remove the outer 20% of the total bone area, i.e. the cortical bone shell. Examples of vertebral sections are shown in electronic supplementary material, figure S3.

Diaphyseal structural properties examined here included total subperiosteal area (TA), medullary area (MA), cortical area (CA) and polar section modulus (Z_p). Z_p is a measure of torsional and (twice) average bending strength [40], and is therefore the most appropriate geometric parameter for assessing overall diaphyseal strength. In addition to analyses of Z_p in individual sections, age changes in the ratio of femoral/humeral Z_p were also assessed, as this index has been shown to relate to behaviour (degree of terrestriality/arboreality) in gorillas [39,41]. The ratio was logged, following previous protocols [38]. Volumetric cortical bone mineral density (vBMD, g/cm^3: BMC/volume of cortical bone in the section) was also assessed. Finally, a pQCT parameter that combines Z_p with bone mineral density distribution in the section, referred to as the polar 'strength-strain index', or SSI_p [37], was included in comparisons.

The vertebral parameter extracted from pQCT scans was volumetric trabecular BMD (vBMD), determined for the inner 80% of the vertebral body (see above and electronic supplementary material, figure S3). Vertebral BMD is highly correlated with vertebral strength [42]. All properties were calculated by internal pQCT software.

(c) Analyses

Least-squares regressions of structural parameter values against age were run for each property within sex. Both linear and quadratic models were tested, with the best fitting model chosen on the basis of improvement in adjusted squared multiple r and AIC (Akaike information criterion) values. A significance level of 0.05 was used in all analyses. Analysis of covariance was also used to assess whether there were any significant differences in the rate of change with age (regression slope) between sexes.

To test whether any secular effects or nonrandom sampling by age of body size characterized the sample, regressions of bone lengths and articular breadths on age were also carried out within sex. No significant ($p < 0.05$) or near-significant ($p < 0.10$) relationships with age were detected. Thus, there was no need to correct for body size in ageing analyses. All statistical analyses were carried out in SYSTAT [43]. All study data are included in electronic supplementary material, table S1.

3. Results

Results of the regressions of structural properties on age are given in table 1. (For a full listing of results for all sections, see electronic supplementary material, table S2.) All properties are better fit by linear regressions, except for MA of the ulna, which is better fit by a quadratic regression in
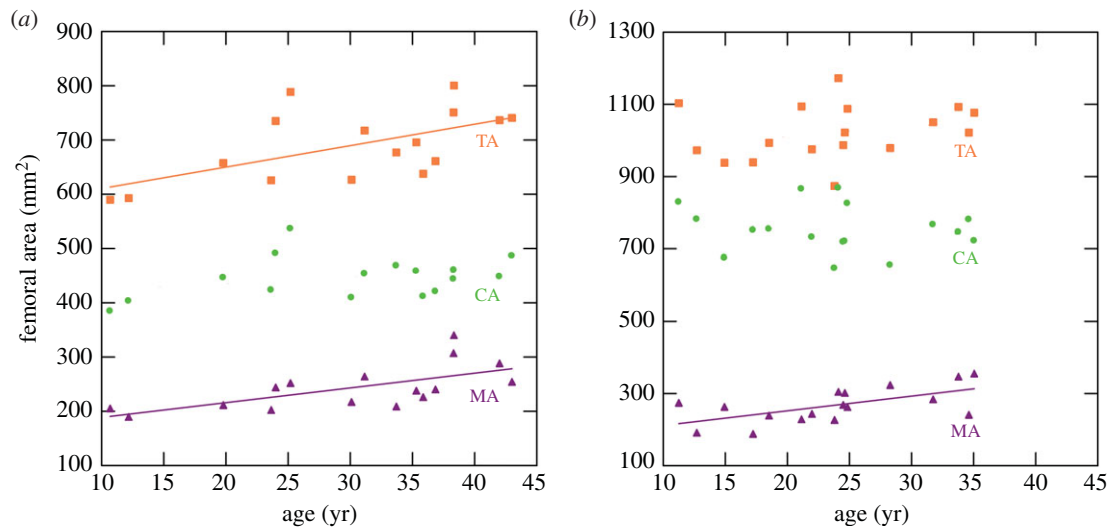
Figure 2. Age changes in femoral midshaft areas in: (*a*) females and (*b*) males. TA (orange squares), total subperiosteal area; MA (purple triangles), medullary area; CA (green circles), cortical area. Least-squares regression lines plotted for significant regressions (table 1). (Online version in colour.)

both sexes. There are no significant differences in regression slopes between the sexes.

All diaphyseal sections except in the humerus show a significant increase with age in MA, i.e. endosteal expansion, in both sexes. Total subperiosteal area (TA) increases significantly with age in the femur and tibia among females and in the radius among males. Cortical area (CA) shows no significant age changes in any section. Plots of TA, MA and CA against age are shown in figure 2 for the femoral midshaft (50%) section.

The polar section modulus, Z_p, increases significantly with age in the femur and tibia among females, paralleling age changes in TA. Males show no significant age change in Z_p for any section. A plot of femoral Z_p versus age is shown in figure 3a. There is no significant age change in the SSI_p parameter, which combines geometric and density properties, in any section in either sex.

Among females, the log ratio of femoral to humeral Z_p increases significantly with age (figure 3b), i.e. femoral to humeral strength increases in older females. The regression on age is strongly affected by low values for the two youngest (10–11 years old) females; however, the age trend is still significant ($p < 0.03$) if these individuals are removed. No similar age trend is apparent in males.

Neither cortical vBMD in diaphyseal sections nor trabecular vBMD in the L3 vertebral body shows any significant change with age in either sex (table 1 and figure 3c,d). There are two high outliers—one male and one female—for vertebral vBMD at approximately 25 years of age (figure 3d). Although peripheral osteophytes and periarticular sclerotic bone were removed prior to analysis, as described above (also see electronic supplementary material, figure S3b), these two specimens exhibit some areas of sclerotic (hypermineralized) trabecular bone within the vertebral body. Removal of these individuals does not appreciably affect regression statistics.

4. Discussion

A qualitative summary of ageing trends for different bone structural properties in humans and mountain gorillas is given in table 2. Results for humans are based on references

given in the text and for mountain gorillas from the present study (table 1 and electronic supplementary material, table S3). This simplified presentation glosses over differences in the timing of events (e.g. the earlier initiation of trabecular versus a compact cortical bone loss in humans) as well as between the sexes (e.g. human females show more medullary expansion than males), but encapsulates general contrasts between the two taxa.

As shown in table 2, Virunga mountain gorillas exhibit some features of skeletal ageing that are similar to those observed in humans. Endosteal resorption leads to a medullary expansion in long bone diaphyses. Some concurrent subperiosteal expansion also takes place, reaching statistical significance in some sections. Together the two trends lead to relative cortical thinning, i.e. reductions in cortical area and thickness relative to external dimensions, especially in females (see electronic supplementary material, table S3). All of these trends have been observed in many living and recent archaeological human samples [1,4–6,44–50]. Reported age trends in diaphyseal cortical area and section moduli (or second moments of area, closely related to section moduli [40]) in humans have been more variable, with both declines and no change or increases observed, varying by skeletal region and potentially related to the degree of mechanical loading [2,44,45,47]. Mountain gorillas show no change in cortical area and no change or an increase in section moduli with ageing, so fall within the continuum of modern humans in terms of geometric remodelling of the diaphysis.

However, mountain gorillas also exhibit some marked differences in patterns of skeletal ageing compared to modern humans. First, mountain gorillas do not decline in bone cortical or trabecular density with ageing, whereas humans consistently do [1–5,44,51,52]. Subperiosteal expansion, leading to stable or increasing geometric parameters of bone strength and rigidity (section moduli and second moments of an area) despite endosteal resorption and cortical thinning, has been seen as partially compensatory to declines in cortical density in humans [4,5,44]. However, combined measures of diaphyseal strength incorporating both geometry and bone mineral density (the 'strength-strain index', SSI, or equivalent) still decline with age in older human females (and to a lesser extent in males) [2,4,5,44]. By contrast, gorillas show no change in SSI_p throughout life in
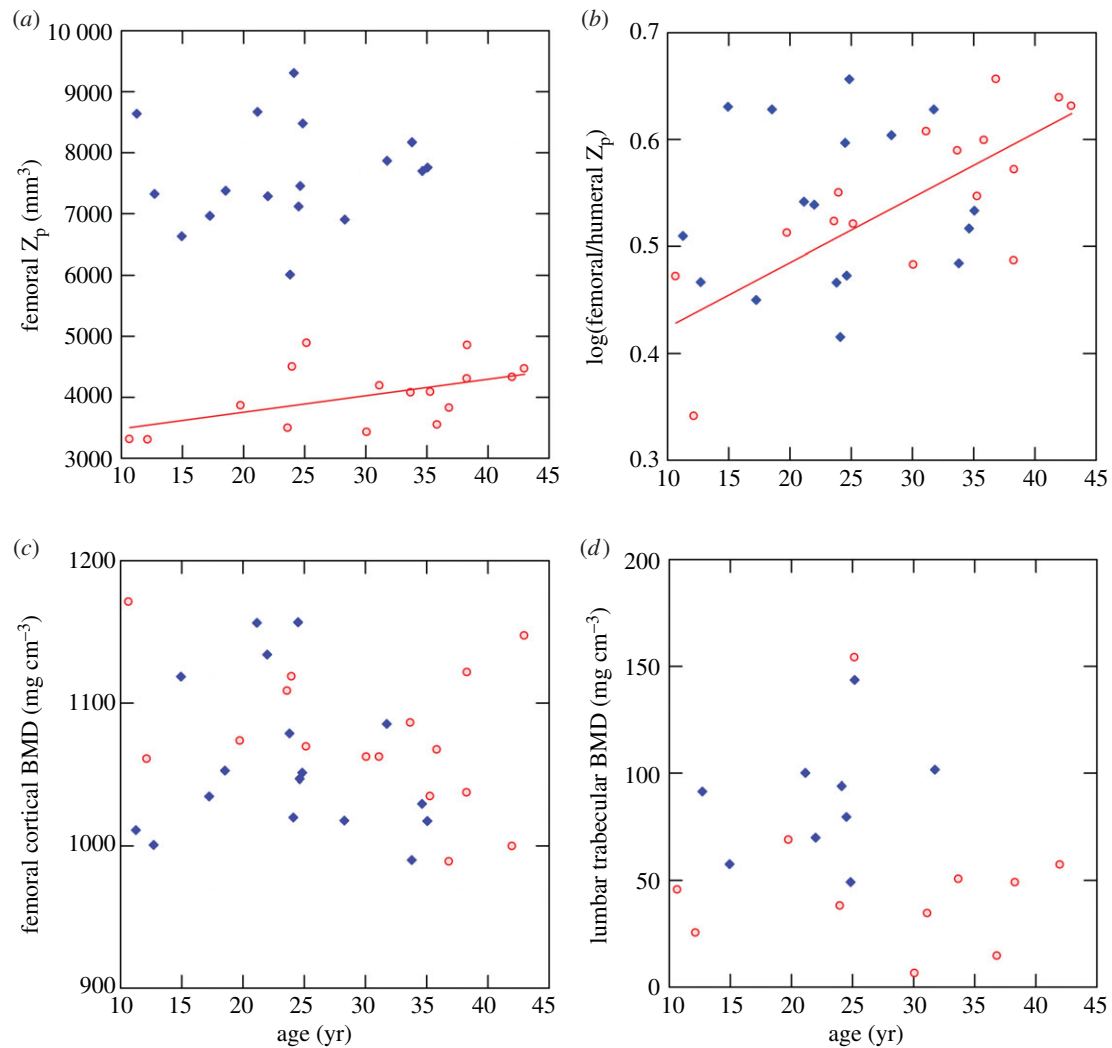
Figure 3. Age changes in section moduli and mineral densities. Red circles, females; blue diamonds, males. Least-squares regression lines plotted for significant regressions (table 1). (a) Femoral midshaft polar section modulus. (b) Log-transformed ratio of femoral to humeral polar section modulus. (c) Femoral midshaft cortical volumetric bone mineral density. (d) L3 vertebra trabecular volumetric bone mineral density. (Online version in colour.)

Table 2. Qualitative comparison of skeletal ageing trends in humans and gorillas.

property[a]	humans[b]	gorillas[b]
TA	+/0	+/0
MA	+	+
CA	0/−	0
%CA	−	−
Z_p	+/0	+/0
SSI_p	−	0
Cort. vBMD	−	0
Trab. vBMD	−	0

[a]See table 1 for property definitions. %CA, CA/TA (see electronic supplementary material, table S3).
[b]+ increases with age; 0 no change with age; − decreases with age. Dual trends = mixed results in different studies or skeletal locations.

any long bone. Trabecular bone density, strongly related to strength [42], also consistently declines in humans (males and females) in both lumbar vertebrae [1,53] and peripheral bone sites [2,4], whereas it is again stable throughout life in gorillas

(in vertebrae). Thus, mountain gorillas show no evidence for a decline in bone strength with ageing.

Second, unlike in humans, there is no evidence that gorilla females suffer greater loss of bone with ageing than gorilla males. Where the sexes have been compared, human females consistently decline more in cortical area and cortical and trabecular bone density than males, with accelerating losses after menopause ([1,4], also see electronic supplementary material, figures S1 and S2). Gorillas show no sex differences in bone loss with ageing, and female gorillas actually exhibit more evidence for positive trends in subperiosteal areas and section moduli.

Differences in hormonal changes with age likely provide the primary explanation for observed differences in skeletal ageing patterns between humans and gorillas. A reduction in estrogen levels following menopause is the predominant factor leading to accelerated bone loss in older human females (Type I Osteoporosis, [9]). While changes in estrogen levels with ageing have not been directly assessed in mountain gorillas, the post-reproductive period in mountain gorillas, as in other nonhuman primates [54], is very short relative to total lifespan [54,55], although fecundity does decline with age [55,56]. Six of the eight gorilla females in the present study over 30 years of age with available reproductive data had given birth within 5.5 years of death, including the oldest

female in the sample (43 years). Data for captive Western lowland gorillas are similar, where all observed females up to 37 years of age had menstrual cycles and most older individuals continued cycling [57]. Thus, it is likely that the protective effects of estrogen against bone loss are maintained in most gorilla females into very old age. Type II Osteoporosis, the slow cumulative loss of bone throughout much of adult life in humans of both sexes [1,9], also does not appear to characterize mountain gorillas. Type II Osteoporosis may be attributable to reduced efficiency of calcium absorption (also see below) as well as hormonal and other factors, including reduced activity level [9]. Variation in activity level and mechanical loading has been suggested to account for at least some of the variation in the geometric remodelling of bone with age observed in human populations [47]. Although overall activity level may decline with ageing in gorillas, as in chimpanzees [26], it is likely that mechanical loading of the skeleton remains above that of more sedentary older modern humans, helping to maintain bone strength.

The observed increase in femoral to humeral strength in mountain gorilla females, but not males, does suggest a sex-specific change in behaviour with ageing, however. Broader comparisons among gorillas indicate that a higher femoral/humeral strength ratio is associated with greater terrestriality, i.e. less use of the trees and thus reduced mechanical loading of the forelimb [41]. Ontogenetic studies also show an increase in this ratio after about 2 years of age in mountain gorillas, when they begin to spend more time on the ground [41,58]. Our current results thus suggest that older adult female mountain gorillas may climb trees less often than younger adult females. A preliminary study of substrate use in Virunga gorillas [59] shows a decline in arboreal bouts after age 8 in females, but not males (electronic supplementary material, figure S4), consistent with this interpretation. This also implies that a sex difference in behaviour previously observed among adult Virunga gorillas, whereby females were more arboreal [58], is characteristic only of young adults (and late adolescents), not older adults, i.e. that locomotor/positional behaviour in the sexes converges towards greater terrestriality with ageing. Avoidance of climbing has also been noted for older chimpanzees from Gombe [26].

The increase in femoral/humeral strength with ageing in female gorillas can be attributed to more positive age changes in the femur in subperiosteal area and section modulus (table 1). This raises the broader question of whether mode of locomotion, for example, bipedality versus quadrupedality, may affect patterns of bone loss and remodelling. One long-term longitudinal study of modern human females found more positive geometric remodelling with ageing in the lower than the upper limb [45], suggesting that there may be a role of weight-bearing in preserving and enhancing bone structural properties. However, another longitudinal study of the radius in post-menopausal women found significant increases in geometric properties, indicating that human upper limb bones may also remodel to (partially) preserve bone strength [44]. Mode of locomotion does affect limb bone strength proportions among primates, both phylogenetically and across ontogeny [38,60–62]. That is, whether weight-bearing or not, bones are adapted to their customary mechanical loadings. Thus, changes in these loadings are likely to influence patterns of bone remodelling, as appears to be the case in adult female mountain gorillas.

Our general ageing results are somewhat at variance with two previous studies of chimpanzees, which reported reduced values for cortical area, BMC and BMD in old females [26–29]. However, as noted earlier, sample sizes in these studies were quite small (1–2 old females in each) and ages were estimated within broad limits. Our results are more similar to a preliminary museum study of larger samples of both chimpanzees and gorillas [30], which found modest if any age-related reductions in bone density or area. No previous study of non-human primates has included combined geometric-density measurements of bone strength.

The differences in skeletal ageing patterns between mountain gorillas and humans and their relationship to reproductive strategies raise some interesting broader evolutionary issues. Osteoporosis in humans is one of a number of traits that has been suggested to possibly result from differing physiological trade-offs among younger and older adults, with adaptations that are favourable during the reproductive period becoming unfavourable post-reproductively when selection pressures are reduced (a form of antagonistic pleiotropy) [12,63]. In the case of bone loss from the skeleton, available mechanisms for activating the release of calcium are critical during pregnancy and lactation to supply the growing fetus and infant, but may be maladaptive later in life with the changing hormonal environment and loss of the protective effects of estrogen [64]. Because of their very short post-reproductive period, gorilla females are not exposed to this environment and are thus largely protected from Type I Osteoporosis. During pregnancy in humans, levels of 1,25-dihydroxyvitamin D increase, enhancing intestinal absorption of calcium [64]. Because reduced levels of vitamin D and impaired calcium absorption with ageing contribute to Type II Osteoporosis [7], continued reproduction into old age in gorillas may also help protect against this mechanism of bone loss, if they undergo the same physiological changes.

Calcium bioavailability is another factor that could influence bone loss or maintenance during the adult lifespan [65]. A study of mountain gorillas in Bwindi Impenetrable National Park, Uganda, found that levels of calcium in the diet were well over those considered to be nutritionally adequate [66], although another study in the same area found that calcium/phosphorus ratios were unbalanced, possibly inhibiting the absorption of phosphorus [67] (but not calcium—see [65]). It is generally believed that levels of calcium in the diet were much higher in early (pre-agricultural) humans than in most modern populations [11,65]. The role of relatively low levels of dietary calcium in promoting osteoporosis in modern humans is contentious [68], but this may also contribute to the observed differences (e.g. in bone mineral density ageing patterns) between gorillas and modern humans, if gorillas are better nourished in this respect. More studies of dietary interactions in wild gorillas and other primates are needed to further evaluate this possibility.

In terms of increased fracture prevalence in older modern humans, the greater lifespan of humans relative to gorillas and other nonhuman primates may also be a factor by providing more absolute time for age-related fractures to accumulate. However, as noted earlier, declines in some bone structural parameters begin in the third and fourth decades in humans [2,3], well within the lifespan of mountain gorillas, while gorillas show no evidence of any such declines. A combination of both living longer and more negative changes in bone structure during that process likely accounts for the increased prevalence of osteoporotic fractures in humans.

The evolution of an increased lifespan and post-reproductive period thus involved some increased skeletal risks for humans, compared to some of our closest phylogenetic relatives. However, in terms of fracture incidence in old age, the risk may have been lower in earlier human populations than in modern, more sedentary populations. Bone loss with ageing is well documented in early historic and archaeological human skeletal samples [48–52]; however, evidence for age-related fractures in samples prior to the past few 100 years is relatively rare [10,49,69,70] (although see [50]). This may be partly a function of difficulty in recognizing such fractures, along with reduced average lifespans [10,69], but it may also result from the development of more advantageous bone structural properties prior to middle and old age (e.g. see [70]). The importance of achieving a high peak bone mass (or strength) early in adulthood, in order to prepare for losses later in life, has been emphasized by many researchers (e.g. [9,71]). Declines in skeletal structural parameters related to bone strength occurred with the adoption of more sedentary lifestyles during the Holocene [72,73]. Even today, geographic variation in age-related fractures parallels variation in activity level [8]. Greater vulnerability to age-related fractures among many modern human populations may be the combined result of both an unusual life history involving a long post-reproductive period during which bone is lost, and a less active lifestyle that stimulates less bone apposition earlier in life.

5. Conclusion

Wild Virunga mountain gorilla adults demonstrate some of the same age-related trends in long bone diaphyseal structure observed among humans, including endosteal resorption coupled with some periosteal apposition. However, unlike humans, mountain gorillas do not decline with age in either cortical or vertebral trabecular bone density, thereby preserving bone strength into old age. There is also no sex difference in patterns of skeletal ageing in gorillas (except for a more positive change in bending strength in some sections in females), in contrast with humans. The difference in skeletal ageing trajectories between the taxa is likely attributable to the lack of a significant post-reproductive period in gorillas, possibly also in combination with an active lifestyle. Studies such as this one of phylogenetically and physiologically close taxa living under natural conditions are valuable in highlighting the distinctiveness of the modern human ageing pattern and its evolutionary context.

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