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Age-related variation in limb bone diaphyseal structure among Inuit foragers from Point Hope, northern Alaska

I. J. Wallace · A. Nesbitt · C. Mongle · E. S. Gould · F. E. Grine

Abstract

Summary Age-related deterioration of limb bone diaphyseal structure is documented among precontact Inuit foragers from northern Alaska. These findings challenge the concept that bone loss and fracture susceptibility among modern Inuit stem from their transition away from a physically demanding traditional lifestyle toward a more sedentary Western lifestyle.

Introduction Skeletal fragility is rare among foragers and other traditional-living societies, likely due to their high physical activity levels. Among modern Inuit, however, severe bone loss and fractures are apparently common. This is possibly because of recent Western influences and increasing sedentism. To determine whether compromised bone structure and strength among the Inuit are indeed aberrant for a traditional-living group, data were collected on age-related variation in limb bone diaphyseal structure from a group predating Western influences.

Methods Skeletons of 184 adults were analyzed from the Point Hope archaeological site. Mid-diaphyseal structure was measured in the humerus, radius, ulna, femur, and tibia using CT. Structural differences were assessed between young, middle-aged, and old individuals.

Results In all bones examined, both females and males exhibited significant age-related reductions in bone quantity. With few exceptions, total bone (periosteal) area did not significantly increase between young and old age in either sex, nor did geometric components of bending rigidity (second moments of area).

Conclusions While the physically demanding lifestyles of certain traditional-living groups may protect against bone loss and fracture susceptibility, this is not the case among the Inuit. It remains possible, however, that Western characteristics of the modern Inuit lifestyle exacerbate age-related skeletal deterioration.

Introduction

People in Western industrialized societies are at risk of a variety of diseases that are uncommon in forager (hunter-gatherer) societies. Such diseases are thought to result from individuals in industrialized societies being incompletely or inadequately adapted to the novel conditions associated with such environments [1, 2]. A potential example of such a disease is osteopenia, a disorder of diminished bone quantity and quality, which becomes osteoporosis when bone structure is compromised to predispose to fracture.

Skeletal fragility is most prevalent among older individuals, although its manifestation reflects cumulative exposure to risk factors throughout the course of life. Among the principal environmental risks is physical inactivity. Maintaining healthy bones requires that the skeleton be subjected to mechanical loading. Growing bones that are routinely loaded by physical activity often become strong, whereas bones that are insufficiently loaded remain slender and frail [3]. Loading-induced bone gains achieved during growth can be preserved and enhanced into older age if individuals remain active, but these gains will erode without continued loading

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[4]. Thus, the occurrence of compromised bone structure in industrialized societies is thought to be due in large part to our skeletons being poorly adapted to our increasingly sedentary lifestyles [2, 5–7].

Fragility fractures are indeed uncommon among forager groups and other subsistence-level societies, even among the most elderly members of these populations [8, 9]. Yet, like most people, foragers experience some degree of age-related bone loss and diminished tissue quality [10, 11]. A prominent explanation for this apparent paradox is that adequate structural (whole bone) strength is preserved throughout life, despite bone deterioration in later decades, due to mechanically optimal changes in cortical bone geometry engendered by lifelong habitual physical activity [12, 13]. In many people, elements of the appendicular skeleton undergo endosteal bone resorption and concomitant marrow cavity expansion with aging that outpaces periosteal bone apposition. However, the rate of periosteal expansion is expected to be somewhat accelerated among foragers as a result of frequent skeletal loading. This would compensate mechanically for age-related endosteal resorption and tissue quality degeneration by limiting net bone loss and maintaining the geometric components of structural resistance to loading.

However, there is at least one group of traditionally foraging peoples, the Inuit of northern Alaska, Canada, and Greenland, among whom fragility fractures have been reported to be common [14–16]. The Inuit also experience a greater severity of bone loss with age compared to other groups [17, 18]. On the face of it, this would seem to contradict the concept that osteopenia and osteoporosis arise primarily from Western lifestyle factors. However, most data on Inuit bone health come from modern communities that have experienced various degrees of lifestyle transition as a result of recent Western economic and social influences. Physical activity levels have declined due to less engagement in traditional subsistence activities and greater use of motorized vehicles, and consumption of traditional foods has decreased in favor of market foods deficient in nutrients vital to bone such as vitamin D and calcium [15, 19, 20]. In this light, compromised bone structure and strength among modern Inuit may actually be seen as evidence of a link between Westernization and diminished skeletal health. Ultimately, in order to determine whether Inuit bone loss and fracture susceptibility are indeed aberrant compared to groups practicing traditional foraging lifestyles, data on age-related variation in bone structure prior to Western influences are needed.

In this study, we examined variation in limb bone diaphyseal geometry with aging in a large sample of precontact Inuit foragers from the Point Hope archaeological site located on the northwestern coast of Alaska, roughly 200 km north of the Arctic Circle. Excavations at Point Hope between 1939 and 1941 uncovered some 500 human skeletons, ruins of over 500 dwellings, and more than 10,000 artifacts [21], which together provide a wealth of information on the biology and lifestyle of these Arctic foragers. Point Hope has been inhabited on a nearly continuous basis for roughly the past two millennia. However, the majority of the archaeological human skeletons derive from two temporally distinct cultural periods, the Ipiutak (ca. 1600 to 1100 years BP) and the Tigara (ca. 800 to 300 years BP). Like in many traditional Arctic forager societies, subsistence at Point Hope centered on the exploitation of sea mammals such as seals, walruses, and whales, in addition to caribou, fish, birds, and other animals [21–23]. Foraging would have been done on foot, in small boats, or with sleds and involved various traditional tools including harpoons, spears, bows and arrows, and stone carcass-processing implements [21, 22]. As is typical among traditional-living Inuit, there was likely a sexual division of foraging effort, such that men would have been primarily responsible for hunting, while women processed and transported animals taken by hunters and would have been responsible for gathering other sources of food [22]. For both sexes, life at Point Hope would have been very physically demanding, as indicated by ethnographic and energy expenditure data from Inuit engaging in traditional subsistence activities [22–25]. Thus, we predicted that the Point Hope Inuit would exhibit a pattern of bone structural variation with aging characterized by sustained periosteal expansion and the maintenance of bone quantity and structural rigidity [12, 13]. If so, the results of this study would support the idea that severe bone loss and skeletal fragility among modern Inuit relate to their transition from traditional foraging to a more Western lifestyle.

Materials and methods

Skeletons of 184 adult individuals were selected for analysis from the Point Hope archaeological collection housed at the American Museum of Natural History. All skeletons originated from either the Ipiutak or Tigara cultural periods (n=38 and 146, respectively). Selection criteria included possession of a complete femur, tibia, humerus, radius, and ulna; fusion of long bone epiphyses; and preservation of the os coxae to determine sex and age. Individuals displaying signs of skeletal pathologies (e.g., trauma) were not excluded from analysis unless those pathologies resulted in marked distortion of limb bone diaphyses.

Sex assignment was based on a suite of reliable dimorphic characteristics of the pelvis and skull, particularly highly diagnostic aspects of the pubis that alone yield >96 % accuracy [26]. Age estimation was based on a combination of standard osteological indicators, including metamorphosis of the symphyseal surface of the pubis and the auricular surface of the ilium [26]. This combination of indicators provided sufficiently precise estimates to enable the sample to be

divided into three age groups: young (18–29), middle-aged (30–50), and old (>50). The sex and age composition of the sample is presented in Table 1.

A series of linear caliper measurements was taken on each skeleton, including limb bone lengths, bi-iliac breadth, and femoral head diameter. Stature for each individual was estimated from lower limb bone lengths using sex-specific regression equations developed for Arctic populations [27]. Body mass was estimated from femoral head diameter using regression equations from a diverse sampling of human populations, including three sex-specific equations and one combined sex equation [28]. Body mass was also estimated based on stature and bi-iliac breadth using sex-specific regression equations constructed for high-latitude populations [29]. Estimates of body mass obtained from these different equations were averaged.

For each skeleton, limb bone mid-diaphyses were CT-scanned using a LightSpeed VCT scanner (GE Healthcare, Waukesha, WI, USA). Right limb elements were analyzed when available. Mid-diaphyseal regions of interest were defined according to femoral oblique length, maximum humeral and ulnar lengths, and tibial and radial articular lengths. Before scanning, the bones were oriented in standardized anatomical planes and placed in a custom-built rack that allowed all elements from an individual to be positioned together with longitudinal axes aligned in the gantry for a single scan. Specimens were scanned dry, and a bone reconstruction algorithm was used. Final CT images had a pixel dimension of 0.49 mm. Images were saved as DICOM files.

Diaphyseal structural properties were calculated from DICOM files using the BoneJ plugin [30] for ImageJ software (NIH, Bethesda, MD, USA). Parameters measured included periosteal area (Ps.Ar, mm^2), cortical area (Ct.Ar, mm^2), endocortical area (Ec.Ar, mm^2), maximum second moments of area (I_{max}, mm^4), and minimum second moments of area (I_{min}, mm^4). In standard beam analysis, Ct.Ar approximates a bone cross section's internal resistance to axial compression and tension, and I_{max} and I_{min} describe resistance to bending around principal axes [31]. Nevertheless, relating any differences in diaphyseal structural properties between age groups to differences in diaphyseal resistance to loading requires caution since diaphyseal rigidity is determined not only by structural geometry but also by the material properties of the bone tissue, which often deteriorate with aging.

In order to compare the diaphyseal structural properties of individuals and samples of varying body sizes, it was necessary to use some type of size standardization. A relatively simple strategy was to divide structural properties by powers of bone length [13, 31]. Because bone areas are expressed as squares of linear dimensions, they could have been scaled isometrically by dividing by bone length^2. Likewise, second moments of area might have been divided by bone length^4. However, from a biomechanical perspective, the most relevant measure for scaling bone areas is body mass since axial stress in a diaphysis can be predicted to be proportional to axial force. Similarly, second moments of area should be scaled by the product of body mass and bone length since bending stress in a diaphysis is proportional to bending force times its moment arm length. Based on these theoretical considerations, when bone areas and area moments are scaled by factors of bone length, the most appropriate exponents are 3 and 5.33, respectively [31]. Alternatively, estimated body mass could have been used to standardize diaphyseal properties, but this would have introduced a certain degree of error into structural

Table 1 Descriptive statistics for body size and limb bone lengths of Inuit foragers from Point Hope

	Female			Male		
	Young	Middle Age	Old	Young	Middle Age	Old
N	29 [7:22]	51 [11:40]	9 [1:8]	23 [8:15]	58 [9:49]	14 [2:12]
Body mass	54.8±3.6[b]	57.2±4.8[b]	57.6±5.3	64.1±4.6	66.0±6.3	67.0±5.7
Stature	147.4±3.2[a]	149.0±3.9[a]	149.5±5.0	157.8±6.2[b]	159.5±5.5[a]	162.9±4.7[a,b]
Humerus length	27.9±0.9[b]	28.6±1.3[b]	28.2±1.5	30.2±2.0[b]	31.0±1.7	31.7±1.8[b]
Radius length	19.4±0.7[c]	20.0±1.2[c]	19.7±1.2	21.7±1.1[a]	22.0±1.3	22.7±1.4[a]
Ulna length	21.8±0.9	22.4±1.2	21.7±1.8	24.2±1.3[b]	24.4±1.4[a]	25.1±2.0[a,b]
Femur length	39.0±1.6[a]	39.7±1.9[a]	39.9±2.3	42.3±3.0[b]	43.2±2.5[a]	44.6±2.1[a,b]
Tibia length	30.2±1.4	30.9±2.0	31.0±2.0	32.7±2.2[b]	33.7±2.2	34.7±1.7[b]

Numbers in brackets indicate the ratio of individuals from the Ipiutak period relative to the Tigara period. Means are shown±standard deviations. Body mass is reported in kilograms and stature and bone lengths are reported in centimeters. Means with the same superscripts differ significantly. Females and males were analyzed separately

[a] Fisher's LSD test $p \leq 0.05$

[b] Fisher's LSD and Tukey-Kramer tests $p \leq 0.05$

[c] Games-Howell test $p \leq 0.05$

analyses. Therefore, we chose to divide diaphyseal properties by the biomechanically suitable allometric factors of bone length.

A thorough examination of tissue composition was beyond the scope of this study since our interest was to explore the skeletal effects of habitual physical activity, and the primary response of bone to loading is through alterations in structural geometry rather than material properties [4]. Nevertheless, to achieve some sense of the degree to which tissue quality varied between the age groups, we analyzed unpublished histomorphometric data from a subset of our skeletal sample that were collected in the early 1980s by Sara Laughlin using the bone core technique [32]. Briefly, small cylindrical bone volumes (4-mm diameter) were drilled and removed from the anterior cortex of a femoral mid-diaphysis from 171 individuals and then scanned using ^{125}I photon absorptiometry. Bone mineral content measured from scans was standardized by cylinder length to calculate the bone mineral index (gm/cm^2). This is a direct measure of intracortical porosity and mineral content, which are the primary determinants of bone tissue strength.

Statistical evaluation of differences between age groups was conducted with ANOVA followed by Fisher's least significant difference (LSD) and Tukey-Kramer (TK) multiple comparisons tests using SPSS software (Version 20; IBM Corp., Armonk, NY, USA). Females and males were analyzed separately. The Shapiro-Wilk test was used to determine if the data were normally distributed. The Levene's test was used to assess the equality of group variances. When the equal variances assumption was violated, a Games-Howell (GH) multiple comparisons test was carried out. In some instances, data were log-transformed or rank-transformed in order to improve normality and/or the homogeneity of variances. Statistical significance was judged using a 95 % criterion ($p \leq 0.05$), and tests were two-tailed. Relative differences between group means were calculated as percent difference±standard deviation of the sampling distribution of the relative difference. Graphical representations of data were created using SigmaPlot (Version 9.0; Systat Software Inc., San Jose, CA, USA).

Results

Body size and limb bone length attributes of the Point Hope Inuit sample, separated by sex and age, are recorded in Table 1. Group parameters for unstandardized limb bone diaphyseal structural properties are recorded in Table 2. For both females and males, significant differences were detected among age groups in estimated body mass, estimated stature, and/or bone lengths (Table 1), which highlight the need for size standardization of diaphyseal structural data in order to identify biomechanically relevant differences in bone

geometry among age groups. Relative group differences in size-standardized diaphyseal structural properties are presented in Table 3.

In the humerus, both females and males displayed significant decreases in cortical bone quantity with aging (Table 3; Fig. 1). Compared to young individuals, old females had 16.2 ±7.3 % lower cortical area (TK: $p=0.043$) and old males had 23.2±4.7 % lower cortical area (TK: $p<0.0001$). In both sexes, a significant decline in bone quantity was detectable by middle age (TK: $p=0.020$ for females, $p<0.01$ for males). Females exhibited greater age-related marrow cavity expansion compared to males. For example, old females had 60.5± 15.4 % larger endocortical area relative to young females (TK: $p<0.001$), while the relative difference among males was only 18.3±12.1 % (LSD: $p=0.11$). Similarly, endocortical area of middle-aged females was 30.6±7.6 % bigger than that of young females (TK: $p<0.001$), but among males, the relative difference was negligible. However, endocortical expansion among females was coupled with a significant 12.5±3.9 % increase in periosteal area between young and old age (LSD: $p=0.037$), whereas males exhibited no significant age-related enlargement of periosteal area. Old males had 21.2±8.7 % lower maximum second moments of area (GH: $p=0.050$) and 23.6±8.6 % lower minimum second moments of area (LSD: $p=0.029$) compared to young individuals. Among females, second moments of area did not significantly vary with age.

In the radius and ulna, both females and males again displayed significantly diminished bone quantity with aging (Table 3; Fig. 1). In females, cortical area in the radius decreased 8.2±4.1 % by middle age (LSD: $p=0.042$) due primarily to a 33.5±8.5 % increase in endocortical area (TK: $p<0.01$). Similarly, in female ulnae, a 34.2±7.8 % enlargement of endocortical area by middle age (GH: $p<0.001$) led to 9.2±4.0 % lower cortical area (TK: $p=0.015$). In males, between middle and old age, cortical area declined by 11.1± 4.1 % in the radius (LSD: $p=0.035$) and by 7.5±6.8 % in the ulna (LSD: $p=0.033$). This decreased bone quantity in old age was associated with a significant 24.4±11.9 % increase in endocortical area in the ulna (TK: $p=0.036$) and a nonsignificant 13.9±10.3 % increase in the radius (LSD: $p=$ 0.16). Thus, as for the humerus, age-related marrow cavity expansion was generally greater in females than males. Among females, but not males, periosteal areas and second moments of area of forearm bones increased between middle and old age, particularly in the ulna, although not significantly so. As a result, differences in radial and ulnar cortical areas between young and old females were not as great as differences between young and middle-aged females.

In the femur, as in upper limb elements, bone quantity significantly decreased with age among both females and males (Table 3; Fig. 2). Relative to young individuals, old females had 10.8±4.6 % reduced cortical area (LSD: $p=$ 0.031) and old males had 11.0±4.5 % reduced cortical area

Table 2 Descriptive statistics for unstandardized limb bone diaphyseal structural properties of Inuit foragers from Point Hope

	Females			Males		
	Young	Middle Age	Old	Young	Middle Age	Old
Humerus						
Ps.Ar	232.0±34.8	260.3±33.9	271.3±41.6	328.9±31.7	332.7±47.5	356.7±45.3
Ct.Ar	145.4±20.6	138.9±23.9	126.3±31.0	207.2±30.7	196.5±31.6	185.5±25.8
Ec.Ar	86.6±26.3	121.4±34.9	145.0±44.2	121.7±36.2	136.2±39.3	171.2±41.3
I_{max}	4901.6±1370.1	5466.5±1263.4	5445.0±1524.6	9831.0±2104.2	9725.4±2470.5	10565.3±2403.7
I_{min}	2841.0±887.1	3250.1±894.2	3193.8±1132.4	5565.6±1004.6	5729.2±1621.6	5748.5±1316.3
Radius						
Ps.Ar	83.0±12.2	91.1±13.4	91.9±18.3	111.8±14.0	113.0±16.3	118.7±19.7
Ct.Ar	62.5±9.8008	61.6±10.6	61.1±9.8	79.7±13.2	82.8±14.2	80.3±10.7
Ec.Ar	20.5±5.5	29.5±10.5	30.8±17.2	32.2±8.4	30.3±8.7	38.3±13.9
I_{max}	715.7±253.9	836.5±262.5	929.8±281.6	1244.4±355.2	1298.2±417.3	1410.7±510.4
I_{min}	395.3±108.6	444.8±120.6	484.4±113.5	714.2±194.3	746.5±203.4	787.0±205.2
Ulna						
Ps.Ar	92.3±10.1	100.8±13.0	104.5±16.5	122.4±12.5	124.0±14.8	133.6±17.9
Ct.Ar	71.5±8.4	70.4±10.9	69.0±13.8	91.2±13.4	93.6±12.7	93.3±14.7
Ec.Ar	20.8±5.5	30.4±9.7	35.5±9.6	31.2±8.0	30.4±8.6	40.3±9.0
I_{max}	922.1±239.2	1010.5±300.7	1111.2±325.4	1616.7±431.3	1655.2±476.4	1897.3±619.3
I_{min}	508.6±115.3	621.4±169.7	632.1±247.8	908.9±197.5	961.7±238.3	1063.3±293.0
Femur						
Ps.Ar	448.1±41.8	504.7±53.8	501.1±88.3	558.5±59.8	592.5±62.1	626.5±57.9
Ct.Ar	327.8±30.8	334.6±39.7	317.2±57.5	401.9±44.8	415.4±49.2	420.6±44.0
Ec.Ar	120.3±25.0	170.1±47.7	183.9±72.3	156.6±41.0	177.1±45.6	205.9±53.3
I_{max}	17,433.1±3854.4	20,624.6±4864.2	20,651.3±8478.1	27,655.8±6410.0	30,676.5±7842.7	33,667.9±6583.8
I_{min}	13,188.9±2186.6	16,300.5±3240.4	15,545.3±4485.4	20,016.5±4048.3	22,547.2±4190.3	24,128.7±3604.2
Tibia						
Ps.Ar	328.8±33.8	364.9±38.9	360.6±51.4	418.4±42.2	438.5±47.2	467.0±52.9
Ct.Ar	228.2±24.0	227.5±31.4	204.1±42.2	290.8±40.0	300.5±38.6	307.9±42.5
Ec.Ar	100.6±18.0	137.4±38.2	156.5±51.7	127.7±33.6	138.0±30.0	159.1±39.6
I_{max}	11,877.6±2296.0	14,020.5±2906.7	13,683.9±4471.7	20,842.7±5031.3	22,568.3±5073.6	26,010.8±6804.2
I_{min}	5247.1±1225.2	5984.0±1337.0	5219.2±1486.7	8000.0±1701.2	8852.6±2076.5	9527.8±1824.6

Means are shown±standard deviations

Ps.Ar periosteal area (mm^2), *Ct.Ar* cortical area (mm^2), *Ec.Ar* endocortical area (mm^2), I_{max} maximum second moments of area (mm^4), I_{min} minimum second moments of area (mm^4)

(TK: $p=0.050$). Contributing to this decline in bone quantity among females was a 40.1±15.5 % expansion of endocortical area between young and old age (TK: $p<0.01$). A large and significant increase in endocortical area among females (32.9 ±6.2 %) occurred by middle age (TK: $p<0.0001$), but cortical area did not significantly decline by this time due to a concomitant significant increase of 6.1±2.6 % in the periosteal area (TK: $p=0.050$). Minimum second moments of area also increased significantly by 11.3±5.1 % among females between young and middle age (LSD: $p=0.037$). Between middle and old age, however, periosteal area did not vary significantly among females. The significant reduction in cortical area between young and old age among males was associated

with a relatively small (compared to females) and non-significant 12.3±9.8 % increase in endocortical area (LSD: $p=0.17$) without a significant attendant difference in periosteal area. Second moments of area decreased between middle and old age to a similar degree in both sexes, although not significantly so.

In the tibia, significant age-related deterioration of bone quantity also occurred among both females and males (Table 3; Fig. 2). Old females had 17.4±6.1 % lower cortical area than young females (TK: $p=0.020$) and old males had 13.1±5.8 % lower cortical area than young males (LSD: $p=0.049$). Among females, bone quantity reduction was driven by a 26.5±6.1 % enlargement of endocortical area between

Table 3 Relative differences in size-standardized limb bone diaphyseal structural properties between age groups of Inuit foragers from Point Hope

	Females			Males		
	Middle Age vs. Young	Old vs. Middle Age	Old vs. Young	Middle Age vs. Young	Old vs. Middle Age	Old vs. Young
Humerus						
$Ps.Ar$	4.8±3.5	7.3±3.3	12.5±3.9[a]	−7.4±4.8	−0.1±4.3	−7.5±5.6
$Ct.Ar$	−10.6±3.6[b]	−6.3±8.1	−16.2±7.3[b]	−12.3±4.6[b]	−12.4±3.4[b]	−23.2±4.7[b]
$Ec.Ar$	30.6±7.6[b]	22.9±11.7[b]	60.5±15.4[b]	0.8±9.2	17.4±9.5	18.3±12.1
I_{max}	−0.4±6.3	3.0±6.6	2.6±7.4	−16.6±8.4	−5.6±5.9	−21.2±8.7[c]
I_{min}	0.9±7.1	2.2±9.9	3.1±11.0	−13.5±8.1	−11.7±6.5	−23.6±8.6[a]
Radius						
$Ps.Ar$	2.1±3.9	4.7±7.8	6.9±7.9	−3.8±3.9	−4.4±4.1	−8.0±4.7
$Ct.Ar$	−8.2±4.1[a]	3.9±9.0	−4.6±8.2	−0.9±4.4	−11.1±4.1[a]	−11.9±5.0[a]
$Ec.Ar$	33.5±8.5[b]	6.4±20.9	42.1±27.4[a]	−11.0±7.1	13.9±10.3	1.4±10.4
I_{max}	5.8±9.1	17.7±14.5	24.5±15.0	−5.1±7.7	−9.2±8.0	−13.8±9.2
I_{min}	−0.6±7.6	18.2±14.8	17.5±14.9	−4.3±6.8	−10.6±6.6	−14.4±7.9
Ulna						
$Ps.Ar$	0.5±3.7	15.5±8.8	16.2±9.1	−1.4±4.1	0.4±6.8	−1.1±7.0
$Ct.Ar$	−9.2±4.0[b]	7.4±6.7	−2.5±6.5	0.0±4.7	−7.5±6.8[a]	−7.4±7.4
$Ec.Ar$	34.2±7.8[c]	34.4±20.3	80.4±27.1[c]	−5.5±7.0	24.4±11.9[b]	17.5±12.1
I_{max}	−5.5±7.5	32.1±15.6[b]	24.8±15.5[a]	−1.2±8.4	−1.5±11.3	−2.6±12.1
I_{min}	4.2±8.4	22.2±17.3	27.4±18.8	1.3±8.3	−1.6±15.0	−0.3±15.8
Femur						
$Ps.Ar$	6.1±2.6[b]	−3.1±3.0	2.8±3.4	0.0±3.3	−4.4±3.6	−4.5±4.3
$Ct.Ar$	−3.7±2.9	−7.3±4.7	−10.8±4.6[a]	−2.5±3.6	−8.7±3.8[a]	−11.0±4.5[b]
$Ec.Ar$	32.9±6.2[b]	5.4±11.9	40.1±15.5[b]	6.3±6.1	5.6±8.4	12.3±9.8
I_{max}	6.0±4.9	−6.6±6.6	−1.0±7.5	−0.8±5.4	−7.5±6.2	−8.2±7.2
I_{min}	11.3±5.1[a]	−9.7±5.8	0.5±6.5	1.0±6.4	−10.8±6.1	−9.9±7.7
Tibia						
$Ps.Ar$	4.2±3.5	−3.6±3.4	0.4±3.6	−4.5±4.0	−3.3±4.1	−7.7±4.8
$Ct.Ar$	−5.6±4.0	−12.5±6.9	−17.4±6.1[b]	−6.3±5.0	−7.3±4.6	−13.1±5.8[a]
$Ec.Ar$	26.5±6.1[b]	11.4±11.3	40.8±14.2[b]	−0.5±5.9	5.3±8.8	4.8±9.6
I_{max}	7.4±7.1	−10.7±6.6	−4.1±6.2	−8.1±7.8	−4.4±8.4	−12.2±9.5
I_{min}	2.9±7.0	−17.0±7.8	−14.6±8.3	−7.9±7.7	−9.5±6.3	−16.7±8.4

Relative differences between groups were calculated as percent difference±standard deviation of the sampling distribution of the relative difference. Females and males were analyzed separately. Differences with superscripts indicate significant differences between age groups

Ps.Ar periosteal area, *Ct.Ar* cortical area, *Ec.Ar* endocortical area, I_{max} maximum second moments of area, I_{min} minimum second moments of area

[a] Fisher's LSD test $p \leq 0.05$

[b] Fisher's LSD and Tukey-Kramer tests $p \leq 0.05$

[c] Games-Howell test $p \leq 0.05$

young and middle age (TK: $p < 0.001$) and a 40.8±14.2 % enlargement between young and old age (TK: $p < 0.01$). In the tibia, as in all other elements, males displayed less age-related marrow cavity expansion than females. Periosteal area did not significantly vary with aging in either sex. Second moments of area decreased between young and old age in both sexes, but the differences were not statistically significant.

Tissue quality significantly deteriorated with age among females but not males (Fig. 3). Among females, mineral content index in the femoral mid-diaphysis decreased by 8.2±2.6 % between young and middle age (TK: $p < 0.01$) and by 14.6±7.4 % between young and old age (LSD: $p = 0.036$).

Discussion

Measurements of age-related variation in limb bone geometry among precontact Inuit foragers from Point Hope, northern
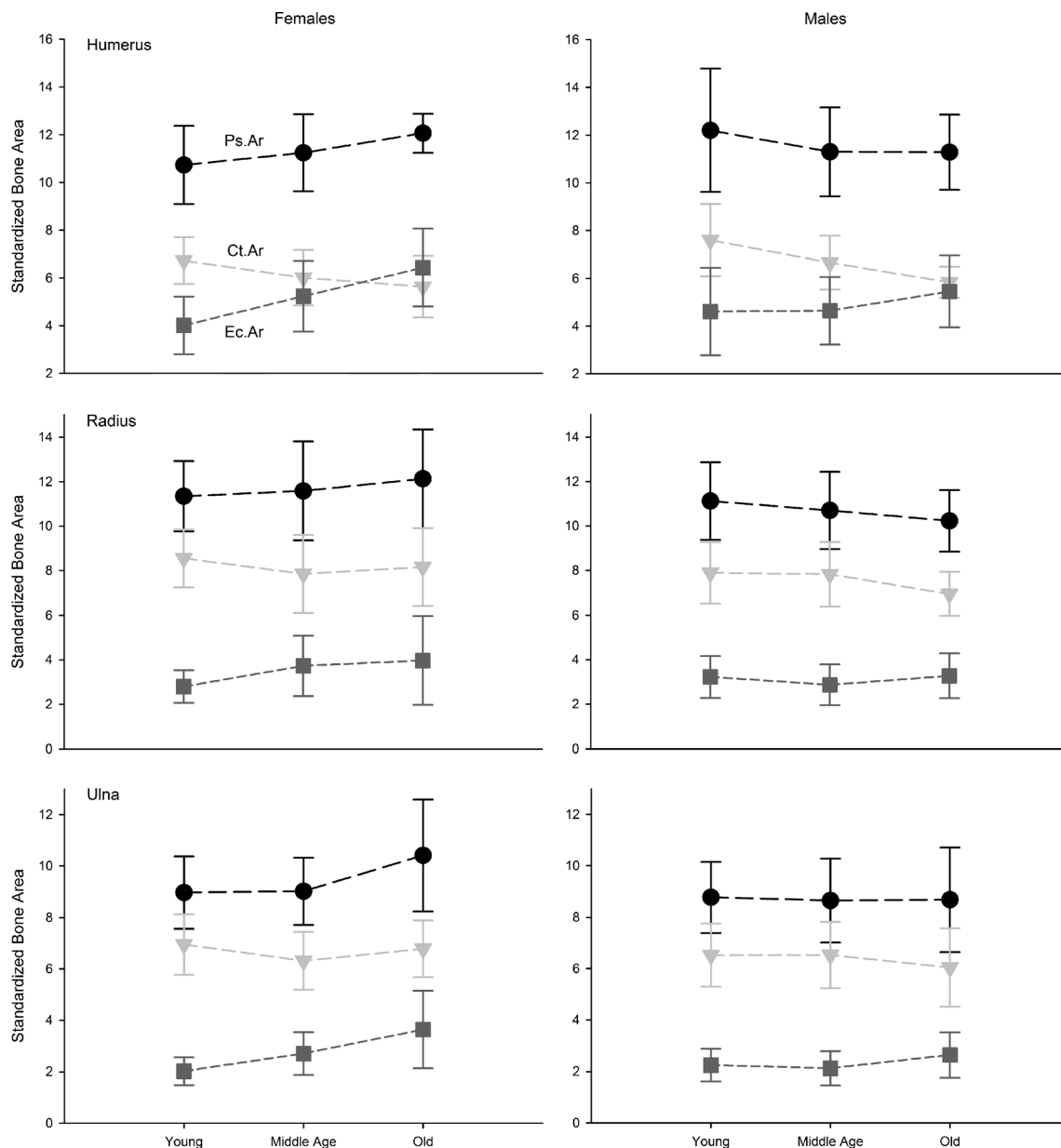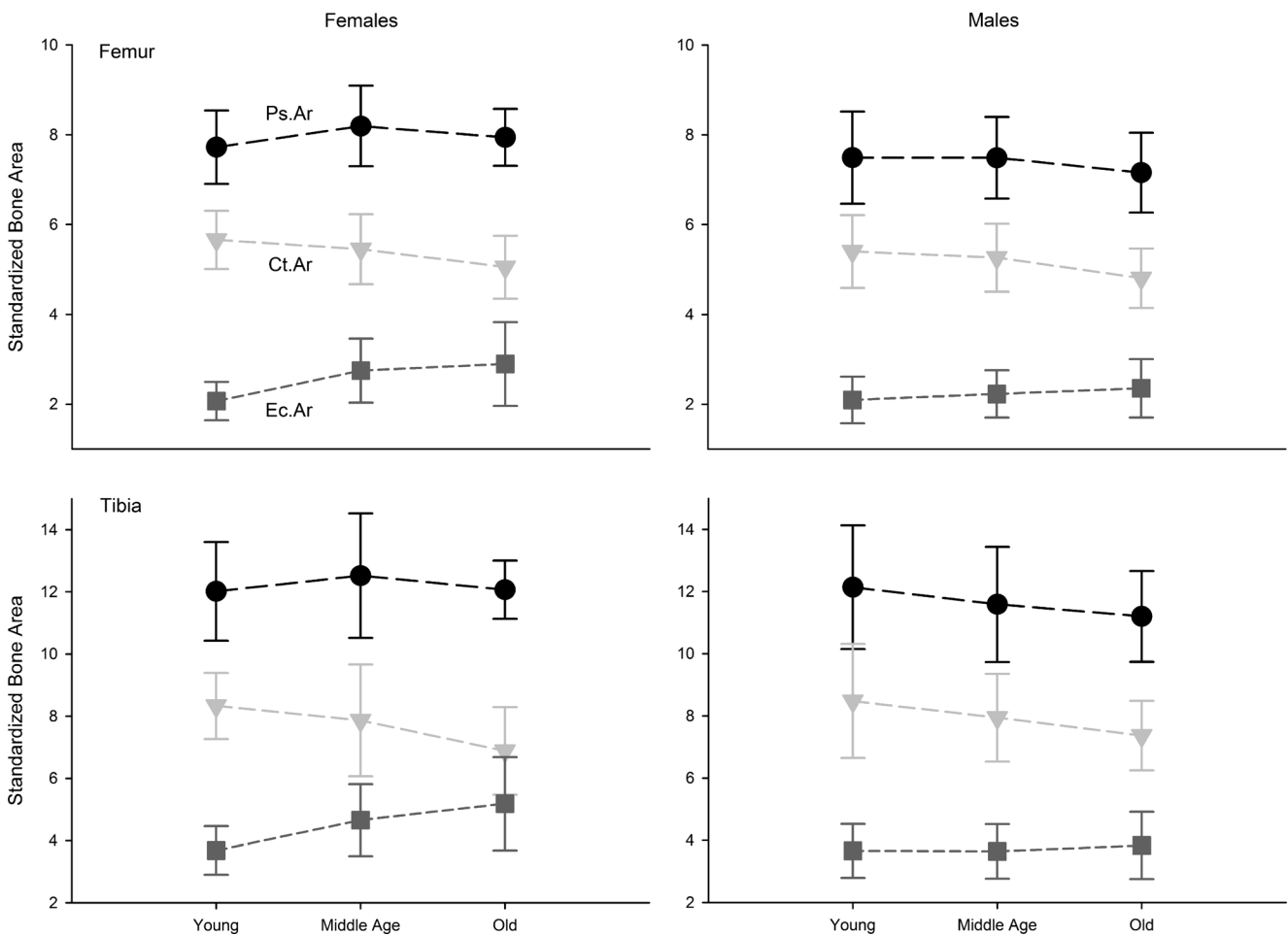
Fig. 1 Variation with aging in size-standardized bone areas of upper limb mid-diaphyseal cross-sections among Inuit foragers from Point Hope (means±standard deviations). *Circles* equal mean periosteal area (Ps.Ar), *triangles* equal mean cortical area (Ct.Ar), and *squares* equal mean endocortical area (Ec.Ar). Values were divided by bone length[3] and are reported as values multiplied by 10[3]

Alaska, challenge the view that bone loss and fracture susceptibility among modern Inuit stem primarily from their transition away from a physically demanding traditional foraging lifestyle toward a more sedentary Western lifestyle. Contrary to the prediction that relatively higher physical activity levels among the traditional-living Inuit at Point Hope would promote continuous periosteal apposition and preservation of bone quantity and rigidity throughout life [12, 13], skeletal structure was observed to deteriorate with age just as it does among modern Inuit [15, 17, 18]. In all five limb bones examined in this study, both females and males exhibited significant age-related reductions in diaphyseal cortical bone quantity, suggesting decreased structural resistance to axial loading [31]. With few exceptions, and contrary to expectations, periosteal area did not significantly increase between young and old age in either sex and nor did second moments of area. In males, humeral second moments of area actually decreased significantly with age, implying reduced bending rigidity [31]. In females, age-related deterioration in femoral structure was coupled with a significant decline in tissue quality. These results do not negate the possibility that Western characteristics of the modern Inuit lifestyle exacerbate age-related deterioration in skeletal structure and strength. Rather, they indicate
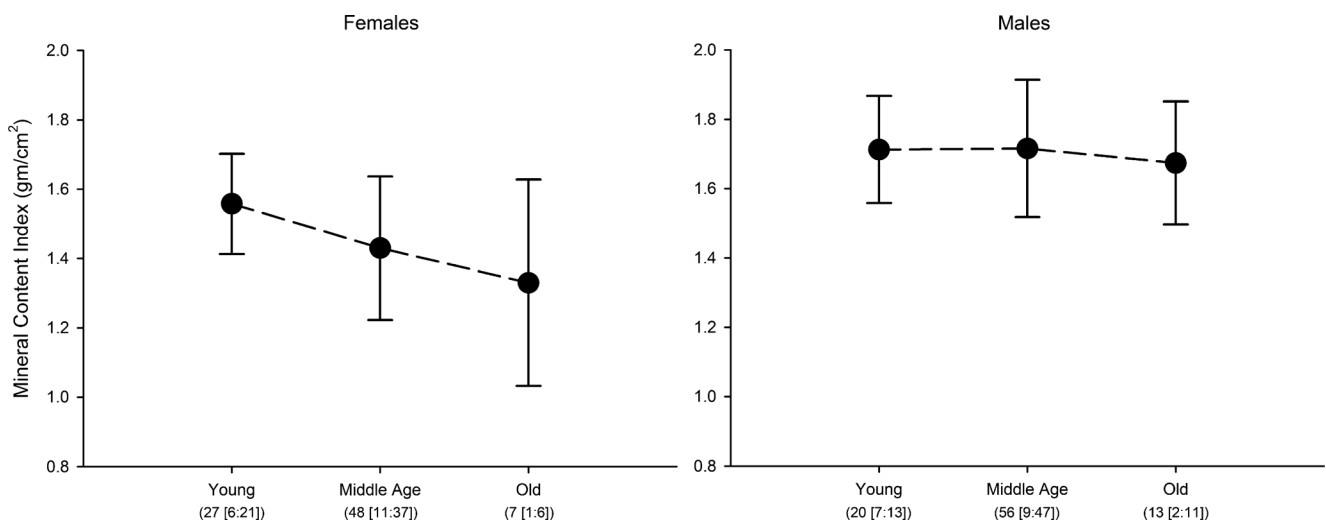
Fig. 2 Variation with aging in size-standardized bone areas of lower limb mid-diaphyseal cross-sections among Inuit foragers from Point Hope (means±standard deviations). *Circles* equal mean periosteal area (Ps.Ar), *triangles* equal mean cortical area (Ct.Ar), and *squares* equal mean endocortical area (Ec.Ar). Values were divided by bone length^3 and are reported as values multiplied by 10^3

simply that bone degeneration with aging is an ancient phenomenon among this group.

Patterns of bone structural variation with aging among Point Hope Inuit bear similarities, as well as differences, with

Fig. 3 Variation with aging in femoral bone tissue mineral content index among Inuit foragers from Point Hope (means±standard deviations). Sample sizes in parentheses. *Numbers in brackets* indicate the ratio of individuals from the Ipiutak period relative to the Tigara period

those previously documented among Western industrialized populations. Consistent with our results, a study of aging patterns in the femur and tibia of urban US adults found that females exhibited a significant age-related decline in bone quantity brought about by marked endocortical expansion with no attendant increase in periosteal area [13]. In contrast to our results, however, US males were found to display less change in bone quantity with age due to moderate periosteal enlargement [13]. Other studies have documented sex-specific differences in age-related variation in bone geometry of both upper and lower limb elements, with many showing greater endocortical expansion and cortical bone loss among females and more periosteal expansion among males [33–35]. Point Hope males generally displayed less endocortical expansion with age than females, but they are distinct from other groups in their complete lack of continued periosteal apposition.

Another notable characteristic of the Point Hope sample is the geometric changes observed among females in weight-bearing lower limb elements compared to non-weight-bearing upper limb elements. Some previous studies have shown that skeletal deterioration with age is less severe in weight-bearing bones than non-weight-bearing bones [36, 37], presumably due to the anabolic (or anti-catabolic) benefits of mechanical loading. This is true for Point Hope males, who exhibited the largest age-related declines in bone quantity and second moments of area in their humeri. Among Point Hope females, however, significant periosteal expansion with age was observed only in the humerus, and the lowest reductions in bone quantity between young and old age were found in the radius and ulna. The underlying causes of these apparent differences in skeletal aging between Point Hope foragers and other populations remain elusive, but could relate to biological (genetic or environmental) differences between population groups and/or methodological differences in study designs. Lack of adequate physical activity is one potential cause that probably can be ruled out for the decelerated periosteal expansion among Point Hope males compared to males from other populations.

Although the results of this study do not support the concept that compromised bone structure stems primarily from skeletons being poorly adapted to environmental conditions that depart from those of non-industrial ancestors [2, 5–7], additional data on skeletal aging and fracture risk from other traditional-living groups are needed to more rigorously evaluate this claim. Human foragers display highly diverse lifeways and occupy a wide range of habitats. Thus, no human group provides a perfect model of the environmental conditions of all foragers. The Point Hope Inuit pushed the limits of human adaptation by inhabiting an Arctic environment where critical nutrients for maintaining bone health were likely scarce. In particular, people living in extreme northern climes are at high risk of vitamin D deficiency due to low sunlight exposure [38], which is frequently associated with secondary hyperparathyroidism, bone loss, and fractures [39]. Dark skin pigmentation of the Inuit may exacerbate this problem [38]. In addition, traditional Inuit diets based largely on animal products are often lacking in calcium [40]. Such nutritional constraints are probably uncommon among forager societies [2]. Thus, it is possible that the skeletal aging patterns of the Point Hope Inuit are atypical for groups practicing a traditional foraging lifestyle. At present, what can be said about bone health among foragers and other subsistence-level societies is that while relatively high activity levels appear to protect against age-related bone loss and fracture risk among certain groups [8, 9, 12], this is not the case in every instance. Even so, compelling evidence does exist that, in general, Western industrial environmental factors negatively affect skeletal structure and strength. For example, in many geographic regions, bone fracture rates are lower in rural than urban populations, and in some cases, lower fracture rates in rural groups are associated with higher bone quantity [41–43]. Moreover, lower fracture rates and higher bone quantity in certain rural groups have been linked with higher levels of physical activity and nutritional quality [41, 44]. While it is questionable that the environmental conditions of modern rural groups approximate those of foragers in general any better than do those of the Point Hope Inuit, that such rural vs. urban trends have been detected among genetically diverse groups inhabiting varying geographic regions is certainly suggestive.

Study strengths and limitations

Few previous studies have documented age-related variation in bone structure among traditional-living foragers, and this is the first study to do so in all five major limb elements of the appendicular skeleton. Furthermore, the number of individuals included in this study surpasses the sample size of any previous analysis of aging effects on skeletal structure in a precontact forager population. Nevertheless, this study has a number of important limitations. First, changes in diaphyseal bone structure with aging were deduced by comparing individuals of different ages; however, being a cross-sectional study, there is no indication of the true sequence of events and strict ontogenetic causality could not be demonstrated. Therefore, inferences of processes underlying structural differences between age groups (e.g., "endocortical expansion") must be considered with some degree of caution. Second, we did not attempt to document the incidence of fragility fractures among the Point Hope Inuit, nor did we analyze bone structure in trabecular-rich regions of the ends of limb bones where such fractures frequently occur. Assignment of fractures observed in archaeological collections to compromised bone structure is problematic for several reasons [9], not the least of which is that it is usually impossible to determine whether

structural diminishment occurred as a result of the fracture or was its cause. Assessment of trabecular morphology is also difficult in archaeological specimens due to regular poor preservation of skeletal microstructure [9]. Third, sample sizes for old individuals were relatively small, perhaps due to typically short lifespans in this population, which limited our statistical power to detect significant differences with other age groups. Fourth, the use of an archaeological collection also has the disadvantage of having to estimate sex and age, the latter of which is more prone to error [26]. Assignment of individuals to one of three gross age categories lowered the resolution with which age-related variation in bone structure could be tracked, but this was a more conservative approach than attempting to estimate age more precisely. Nevertheless, there is a tendency for skeletal aging methods to overestimate age in young individuals and underestimate in old individuals [45], making it possible that some specimens in the middle-aged group were misclassified.

Conflict of interest   None.

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