Structural Changes in the Femur with the Transition to Agriculture on the Georgia Coast

ARTICLE *in* AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY · JUNE 1984

Impact Factor: 2.38 · DOI: 10.1002/ajpa.1330640205 · Source: PubMed

Christopher Ruff
Johns Hopkins Medicine

Wilson C Hayes
Hayes + Associates, Inc.

AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 64:125–136 (1984)

Structural Changes in the Femur With the Transition to Agriculture on the Georgia Coast

CHRISTOPHER B. RUFF, CLARK SPENCER LARSEN, AND WILSON C. HAYES
Orthopaedic Biomechanics Laboratory, Charles A. Dana Research Institute, Beth Israel Hospital and Harvard Medical School, Boston, Massachusetts 02215 (CBR, WCH) and Department of Anthropology, Northern Illinois University, DeKalb, Illinois 60115 (CSL)

KEY WORDS Georgia coast, Subsistence strategy, Femur, Mechanical loadings

ABSTRACT Structural characteristics of the femur are compared in preagricultural (2200 B.C.–A.D. 1150) and agricultural (A.D. 1150–1550) subsistence strategy groups from the Georgia coast. Using an automated technique, cross-sectional geometric properties used in structural analyses (areas, second moments of area) were determined at midshaft and distal to the lesser trochanter in 20 adults from each group. A significant decline in magnitude of almost every geometric property occurs in the agricultural group. The differences between groups are reduced but still significant for many properties after standardizing for bone length differences. In addition, a remodeling of the femoral cortex to one of relatively smaller medullary and subperiosteal diameter, as well as a more circular cross-sectional shape, is characteristic of agricultural femora. Thus, while the relative cross-sectional area of bone remains the same, the spatial distribution of bone area is different in the two groups. The results strongly suggest a relative reduction in mechanical loadings of the femur in the agricultural group, implying different levels and possibly types of activity involving the lower limb in the two groups. The data are also compared with similar data available for the Pecos Pueblo (agricultural) sample. The comparison indicates that types of activity may have been more similar in the two agricultural samples, but that general levels of activity were more similar in the Pecos Pueblo and Georgia coast preagricultural samples.

In a famous study entitled "The Spearman and the Archer: An Essay on Selection in Body Build," Brues (1959) hypothesized several possible relationships between methods of food procurement, energy expenditure, and postcranial body form. While some specific predictions of her model may need to be modified in light of further evidence (Frayer, 1981), her general arguments were important in stimulating interest in cultural–environmental effects on human morphology. In particular, her emphasis on mechanical factors was a relatively novel approach to the study of variation in body structure among recent human populations.

Although many investigators have studied the relationship between human morphology and environment in the intervening years since Brues's study, the study of diachronic changes in postcranial body form through examination of skeletal remains has been largely limited to general body size or stature estimates. In addition, there have been very few studies of single well-defined populations over time periods long enough to encompass major environmental shifts.

The particular environmental change examined in the present study is the transition

Christopher B. Ruff's present address is Department of Cell Biology and Anatomy, Johns Hopkins University Medical School, 725 N. Wolfe St., Baltimore, MD 21205.

Received October 26, 1983; accepted January 31, 1984.

from a primarily hunting-gathering to a primarily agricultural subsistence strategy on the prehistoric Georgia coast. We were especially interested in discriminating between nutritional and mechanical effects on skeletal morphology associated with this subsistence strategy change. We chose the femur for study because it is likely to reflect changes in locomotion and other general activity patterns, as well as specific changes in use of the lower limb. The morphologic characteristics of the femur measured include bone cross-sectional geometric properties which can be used to directly test mechanical hypotheses (Ruff and Hayes, 1983a).

MATERIALS AND METHODS

Skeletal material was obtained from several prehistoric sites located on the Georgia coast (Larsen, 1982). Ceramic and other archaeological evidence from this region indicate a continuous in situ cultural development for at least 3,500 years prior to European contact in A.D. 1550 (DePratter, 1977; Thomas and Larsen, 1979). At approximately A.D. 1150, a transition from hunting–gathering–fishing to a mixed economy incorporating corn agriculture occurred (Larsen, 1982).

Twenty complete intact femora were obtained from each subsistence strategy group. Only individuals predating European contact were used. Approximately equal numbers of males and females and right and left sides were included in each group (also see Table 1). All individuals in the sample were adult, with average ages of death of 25 and 28 years in the agricultural and preagricultural groups, respectively. These figures are not significantly different from the mean ages at death reported by Larsen (1982) for much larger samples from the Georgia coast region. Age estimates were based primarily upon functional dental wear, and sex assignment on pelvic morphology (Larsen, 1982).

Two cross-sectional locations in the femur were selected for analysis—one near midshaft and the other just distal to the lesser trochanter. These correspond exactly to the 50% and 80% locations of the femur defined in detail in Ruff and Hayes (1983a). After careful orientation with respect to anatomical reference planes, bones were sectioned transversely at each location using a fine-toothed band saw. Photographs of the cut cross-sectional surfaces were projected onto a digitizer, and subperiosteal and endosteal surfaces manually traced. The Cartesian coordinates of the boundaries were input to program SLICE (Nagurka and Hayes, 1980), where geometric properties (areas, second moments of area and their orientations) were calculated.

As we have discussed previously (Ruff and Hayes, 1983a), the cross-sectional area of bone [cortical area (CA)] is an appropriate dimension for evaluating resistance of a long bone to axial compressive and tensile mechanical loadings. However, due to bone curvature and other factors, resistance to bending and torsional loadings is generally more critical in assessing long bone strength and rigidity in vivo. These mechanical properties can be evaluated by the relative magnitudes of the second moments of area of a cross section — I (bending) or J (torsional). Second moments of area depend upon both the area of bone and the distribution of bone area, with a more outwardly distributed area resulting in larger values of I and J. A complete list of the geometric properties measured in the present study is included in Abbreviations.

As shown below, there is a significant decline in femoral bone length from the Georgia coast preagricultural to agricultural groups, particularly among females. This is consistent with earlier reported measurements of a much larger sample of femora and other long bones from the Georgia coast region (Larsen, 1981, 1982). In order to test the possibility that observed changes in cross-sectional geometric parameters were due entirely or partly to differences in bone length, some sort of length standardization procedure was necessary.

We have discussed elsewhere some of the difficulties involved in "size" standardization of morphometric data using bone length (Ruff and Hayes, 1983a). Empirical studies of the Georgia coast sample, an archaeological sample from Pecos Pueblo, New Mexico (Ruff and Hayes, 1983a), and a modern autopsy sample indicate that in general, cross-sectional geometric properites and length of human lower limb bones are approximately isometric (Ruff, in preparation). That is, cross-sectional area is approximately proportional to bone length^2, while second moments of area (fourth powers of linear dimensions) are approximately proportional to bone length^4, both within and between population samples. Therefore, in the present study bone lengths to the second and fourth powers were

traced. The Cartesian co-
oundaries were input to
agurka and Hayes, 1980),
properties (areas, second
id their orientations) were

issed previously (Ruff and
e cross-sectional area of
ı (CA)] is an appropriate
uating resistance of a long
ipressive and tensile me-
However, due to bone cur-
r factors, resistance to
mal loadings is generally
sessing long bone strength
o. These mechanical prop-
iated by the relative mag-
ond moments of area of a
(bending) or J (torsional).
of area depend upon both
nd the distribution of bone
outwardly distributed area
· values of I and J. A com-
geometric properties mea-
sent study is included in

, there is a significant de-
one length from the Geor-
icultural to agricultural
ly among females. This is
earlier reported measure-
arger sample of femora and
from the Georgia coast re-
, 1982). In order to test the
bserved changes in cross-
ic parameters were due en-
differences in bone length,
gth standardization proce-
y.
sed elsewhere some of the
ved in "size" standardiza-
tric data using bone length
1983a). Empirical studies of
sample, an archaeological
s Pueblo, New Mexico (Ruff
a), and a modern autopsy
that in general, cross-sec-
properites and length of hu-
bones are approximately
ı preparation). That is, cross-
approximately proportional
while second moments of
rs of linear dimensions) are
oportional to bone length[4],
between population sam-
in the present study bone
ond and fourth powers were

TABLE 1. *Differences in femoral geometric properties in Georgia coast preagricultural and agricultural samples*

Property[1]	Males: Preag. (n = 8) Mean	SEM	Males: Agri. (n = 11) Mean	SEM	Dif	Females: Preag. (n = 12) Mean	SEM	Females: Agri. (n = 9) Mean	SEM	Dif
Max ln. (cm)	450.9	7.9	437.4	3.6	−13.5	440.2	6.5	400.3	5.2	−39.9**
Length' (cm)	424.9	7.9	411.2	3.7	−13.7	415.2	6.0	376.4	5.0	−38.8**
Midshaft										
CA (cm^2)	420.0	24.9	396.1	11.8	−23.9	326.2	16.2	264.2	12.6	−62.0*
MA (cm^2)	147.8	16.1	105.1	7.8	−42.7*	162.2	17.3	100.4	8.0	−61.8*
TA (cm^2)	567.8	20.3	501.2	15.2	−66.6**	488.5	13.8	364.7	17.3	−123.8**
I_{max} (cm^4)	28719	2965	22390	1696	−6329†	18825	1215	11064	993	−7761**
I_{min} (cm^4)	21060	1209	17429	887	−3631*	15460	926	9129	925	−6331**
I_{max}/I_{min}	1.34	0.07	1.28	0.05	−0.06	1.22	0.04	1.23	0.03	0.01
Theta (°)	80.5	5.1	51.2	10.0	−29.3	59.0	10.5	49.4	23.7	−9.6
J (cm^4)	49779	4128	39819	2477	−9960*	34284	2046	20193	1907	−14901**
I_x/I_y	1.28	0.05	1.08	0.05	−0.20*	1.16	0.06	1.03	0.05	−0.13
Subtrochanteric										
CA (cm^2)	404.5	17.1	372.4	9.9	−32.1	328.1	16.2	269.9	9.8	−58.2*
MA (cm^2)	219.7	14.0	141.2	10.4	−78.5***	209.4	24.1	125.2	8.0	84.2*
TA (cm^2)	624.1	12.2	513.6	13.3	−110.5***	537.5	17.0	395.1	13.7	142.4***
I_{max} (cm^4)	39625	2667	26348	1238	−13277***	28153	1687	16405	1171	−11748***
I_{min} (cm^4)	18857	505	14615	804	−4242***	13281	769	7883	566	−5,398***
I_{max}/I_{min}	2.09	0.11	1.82	0.06	−0.27*	2.14	0.09	2.10	0.10	−0.04
Theta (°)	137.4	4.1	143.4	3.1	6.0	143.2	3.1	131.4	3.6	−11.8*
J (cm^4)	58482	3075	40962	1939	−17520***	41434	2334	24287	1648	−17147***

[1]See Abbreviations.
†P < 0.10; *P < 0.05; **P < 0.01; ***P < 0.001.

used to standardize cross-sectional areas and second moments of area, respectively. (Powers of the bone length dimension used to establish cross section positions (length'), rather than maximum bone length, were used here for reasons discussed in Ruff, 1981.) Comparisons between subsistence strategy groups were carried out for both unstandardized and length-standardized properties.

RESULTS

Results of the unstandardized geometric analyses are given in Table 1 and Figures 1 and 2. A significant decline in almost every cross-sectional geometric property of the femur occurs in the agricultural group. Females show greater absolute and relative (percentage) declines than males, particularly in the femoral midshaft section. The percentage decline in medullary area (MA) is larger than that in CA or total subperiosteal area (TA). Thus, CA tends to be relatively more tightly distributed about the section centroid in the agricultural group, with a relatively smaller medullary canal (i.e., the MA/TA ratio is smaller). The declines in the maximum second moment of area (I_{max}), minimum second moment of area (I_{min}), and polar second moment of area (J) in the agricultural group result from both a decline in absolute CA and this inward redistribution of bone area.

The cross-sectional "shape" index I_{max}/I_{min} (Ruff and Hayes, 1983a) shows no significant difference between groups in the femoral midshaft, but a significant decline among males in the subtrochanteric section. This indicates a relatively more circular cross section at this location among agricultural males. The index I_x/I_y, which is a ratio of bending strengths in the A–P to M–L planes, (Ruff and Hayes, 1983a), also shows a significant decline among males in the midshaft section. The decline appears to be present among females as well, but does not reach statistical significance. This indicates a relative reduction in A–P bending strength of the femoral midshaft in the agricultural group. The I_x/I_y ratio for the subtrochanteric section is not shown, since due to the orientation of this section (see Fig. 5) this ratio tends to confuse "shape" differences (I_{max}/I_{min}) with differences in the orientation of greatest bending rigidity (theta). Theta of the subtrochanteric section shows a significant change between groups among females, becoming more A–P oriented (closer to 90°, measured counterclockwise from the lateral side) in the agricultural group. This is associated with an increase among agricultural females in the antetorsion angle of the femoral head and neck from 23 to 32°. (Males of both groups average 23–24° antetorsion.) Changes in theta of the midshaft section are only significant among males, and indicate an orientation of greatest bending rigidity farther from the A–P axis in the agricultural group. This is consistent with the changes in the I_x/I_y ratio for the midshaft section noted above.

Results of the length-standardized analyses are shown in Table 2 and Figures 3 and 4. Ratios and theta are not repeated because their values remain unchanged from Table 1.

In both the midshaft and subtrochanteric sections, standardizing by bone length results in negligible differences in cortical area between subsistence groups, averaging less than two percent. In contrast, length-standardized MA and TA still exhibit declines in the agricultural group, reaching statistical significance in five of eight comparisons (combined sex comparisons of MA and TA are all significant or near-significant [$P < 0.10$]). Thus, while bone area relative to bone length remains approximately constant, the *distribution* of bone area changes, with a relative reduction in both medullary and subperiosteal dimensions in the agricultural group.

Length-standardized second moments of area also show a clear pattern of decline in the agricultural group, although only two comparisons—male subtrochanteric I_{max} and J—reach statistical significance (group differences in female subtrochanteric J are near-significant). Percentage differences between groups in length-standardized properties are similar in males and females, although there

Abbreviations

Max. ln.,	*maximum bone length*
Length',	*bone length used in deriving cross section locations (see Ruff and Hayes, 1983a)*
CA,	*cortical area*
MA,	*medullary area*
TA,	*total subperiosteal area*
I_{max},	*maximum second moment of area*
I_{min},	*minimum second moment of area*
Theta,	*angle between M–L axis and direction of greatest bending rigidity*
J,	*polar second moment of area*
I_x,	*second moment of area about x (M–L) axis*
I_y,	*second moment of area about y (A–P) axis*

from the lateral side) in the
ıp. This is associated with
ng agricultural females in
angle of the femoral head
23 to 32°. (Males of both
3–24° antetorsion.) Changes
idshaft section are only sig-
nales, and indicate an ori-
est bending rigidity farther
s in the agricultural group.
with the changes in the I_x/
idshaft section noted above.
length-standardized anal-
ı Table 2 and Figures 3 and
ta are not repeated because
ıin unchanged from Table 1.
dshaft and subtrochanteric
·dizing by bone length re-
e differences in cortical area
nce groups, averaging less
. In contrast, length-stand-
TA still exhibit declines in
group, reaching statistical
five of eight comparisons
nparisons of MA and TA are
near-significant [P < 0.10]).
area relative to bone length
mately constant, the *distri-*
·ea changes, with a relative
n medullary and subperios-
n the agricultural group.
·dized second moments of
ı clear pattern of decline in
group, although only two
ıle subtrochanteric I_{max} and
al significance (group differ-
subtrochanteric J are near-
entage differences between
-standardized properties are
and females, although there

Abbreviations

ıum bone length
ngth used in deriving cross section
ns (see Ruff and Hayes, 1983a)
l area
lary area
ıbperiosteal area
ıum second moment of area
um second moment of area
between M–L axis and direction of
st bending rigidity
econd moment of area
moment of area about x (M–L) axis
moment of area about y (A–P) axis

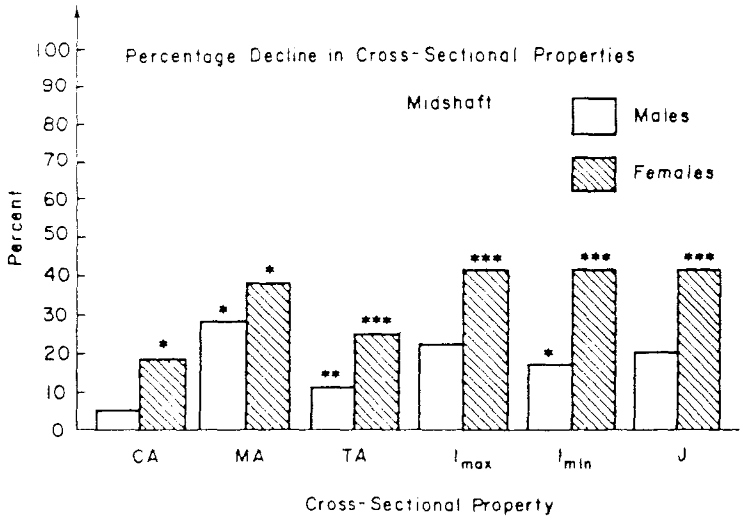

Fig. 1. Percentage decline from Georgia coast preagricultural to agricultural groups in cross-sectional areas and second moments of area of the femoral midshaft {[(preagricultural − agricultural)/preagricultural] · 100} (see Abbreviations). Asterisks indicate statistical significance of t-tests between groups: *P < 0.05; **P < 0.01; ***P < 0.001.

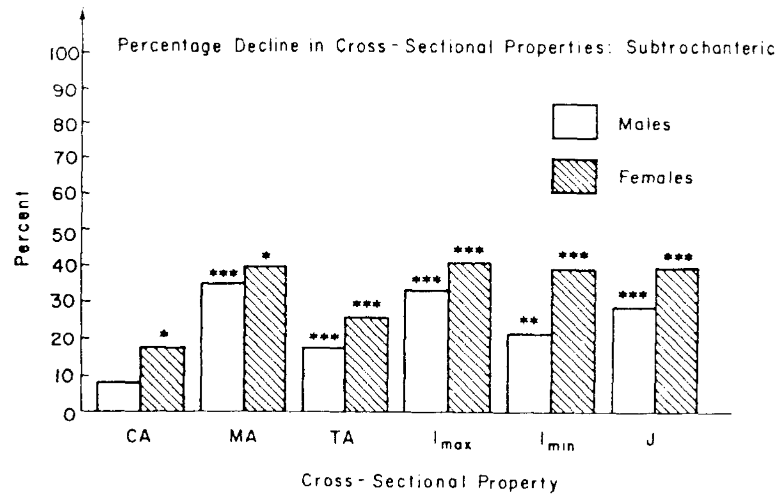

Fig. 2. Percentage decline from Georgia coast preagricultural to agricultural groups in cross-sectional areas and second moments of area of the femoral subtrochanteric section (see Fig. 1). Asterisks indicate statistical significance of t-tests between groups: *P < 0.05; **P < 0.01; ***P < 0.001.

is a slight tendency for females to show greater declines in the midshaft section, and males in the subtrochanteric section.

These differences in cross-sectional geometry of the femur in preagricultural and agricultural groups are summarized in Figure 5. The cross-sectional outlines shown represent typical males from each group, and have been scaled for equal bone lengths. The relative inward contraction of the cortex in the agricultural group is clearly apparent. Greater circularity of the agricultural cross sections is also evident. As stated above, this "shape" difference is more prevalent among males, particularly in the subtrochanteric section.

DISCUSSION

Previous studies of skeletal material from the Georgia coast region have demonstrated a decrease in general body size and robusticity, a reduction in the facial and masticatory apparatus, a decrease in degenerative joint disease, and increases in frequency of periosteal reactions and caries with the transition to agriculture ca. A.D. 1150 (Larsen, 1981, 1982, 1983a,b). With the exception of degenerative joint disease, all of these changes were more marked among females. It was hypothesized that the increase in periosteal reactions was linked to greater population density and increase in spread of infectious diseases following the adoption of agriculture (Larsen, 1982, 1983b), and the other skeletal modifications to both a decline in nutritional level and a decrease in mechanical stress during the agricultural period. The data suggested that females were more affected than males by these changes.

The results of the present study allow a further examination of some of these hypotheses. It was noted earlier (Larsen, 1982) that it is very difficult to distinguish between dietary and mechanical effects on skeletal size and robusticity using traditional osteometric methods. The structural characteristics measured in the present study provide a much more precise evaluation of mechanical function, and thus a clearer differentiation of dietary and mechanical factors.

Two principal alterations in femoral structure with the adoption of agriculture were observed in the present study—a decrease in size, and a redistribution of compact cortical bone within cross sections. When standardized for equivalent femoral length dimensions, the area of bone within cross sections is not significantly different in preagricultural and agricultural groups. However, in the agricultural group, medullary and total subperiosteal areas are relatively reduced, leading to a tighter distribution of bone area about the section centroid. This in turn decreases second moments of area of the sections, and thus bending and torsional strength of the femur. In addition, cross sections of agricultural femora tend to be more circular, with less strongly defined directions of greatest bending rigidity, particularly among males.

TABLE 2. Differences in femoral geometric properties standardized by bone length in Georgia coast preagricultural and agricultural samples

Property[1]	Males					Females				
	Preag.		Agri.			Preag.		Agri.		
	Mean	SEM	Mean	SEM	Dif	Mean	SEM	Mean	SEM	Dif
Midshaft										
CA/ln^2	283.6	14.0	234.5	7.4	0.9	190.2	10.8	186.4	7.8	3.8
MA/ln^2	82.2	8.8	61.8	4.0	−20.4*	93.2	9.1	70.5	5.0	−22.7†
TA/ln^2	315.8	12.5	296.3	7.7	−19.5	283.5	5.9	256.9	10.1	26.6*
I_{max}/ln^4	88.6	8.3	77.9	5.0	−10.7	63.4	3.7	54.8	4.2	8.6
I_{min}/ln^4	65.5	4.8	61.0	2.9	−4.5	51.9	2.5	41.9	3.6	−7.0
J/ln^4	154.1	12.6	138.9	7.5	−15.2	115.4	5.9	99.8	7.8	−15.6
Subtrochanteric										
CA/ln^2	225.0	10.4	220.8	7.1	−4.2	191.5	10.8	190.4	5.7	1.1
MA/ln^2	123.6	11.0	83.6	6.1	−40.0**	120.2	12.7	88.6	6.0	−31.6†
TA/ln^2	348.6	15.7	304.3	9.0	−44.3*	311.7	6.9	279.0	9.2	32.7**
I_{max}/ln^4	124.6	12.2	92.6	5.2	−32.0*	94.7	4.7	81.8	5.9	12.9
I_{min}/ln^4	59.1	4.4	51.5	3.4	−7.6	44.9	2.5	39.2	2.3	−5.7
J/ln^4	183.7	16.2	144.1	8.3	−39.6*	139.6	6.6	121.0	7.8	18.6†

[1]See Abbreviations. Ln = length'. All bone areas multiplied by 10^5, all second moments of area multiplied by 10^8.
†$P < 0.10$; *$P < 0.05$; **$P < 0.01$.

MA/ln²	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
TA/ln²	315.8	12.5	296.3	7.7	−19.5	283.5	5.9	256.9	10.1	−26.6†
I_{max}/ln^4	88.6	8.3	77.9	5.0	−10.7	63.4	3.7	54.8	4.2	−8.6
I_{min}/ln^4	65.5	4.8	61.0	2.9	−4.5	51.9	2.5	44.9	3.6	−7.0
J/ln⁴	154.1	12.6	138.9	7.5	−15.2	115.4	5.9	99.8	7.8	−15.6
Subtrochanteric										
CA/ln²	225.0	10.4	220.8	7.1	−4.2	191.5	10.8	190.4	5.7	−1.1
MA/ln²	123.6	11.0	83.6	6.1	−40.0**	120.2	12.7	88.6	6.0	−31.6†
TA/ln²	348.6	15.7	304.3	9.0	−44.3*	311.7	6.9	279.0	9.2	−32.7**
I_{max}/ln^4	124.6	12.2	92.6	5.2	−32.0*	94.7	4.7	81.8	5.9	−12.9
I_{min}/ln^4	59.1	4.4	51.5	3.4	−7.6	44.9	2.5	39.2	2.3	−5.7
J/ln⁴	183.7	16.2	144.1	8.3	−39.6*	139.6	6.6	121.0	7.8	−18.6†

[1]See Abbreviations. Ln = length[1]. All bone areas multiplied by 10^5, all second moments of area multiplied by 10^8.
†P < 0.10; *P < 0.05; **P < 0.01.

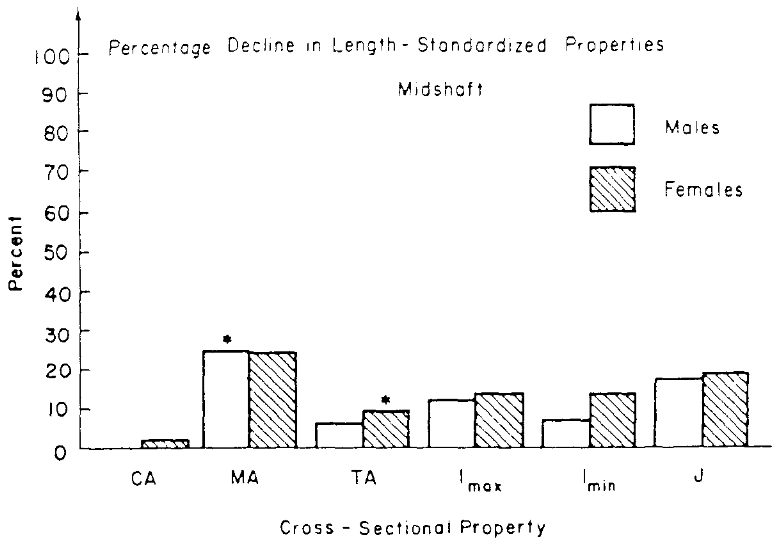

Fig. 3. Percentage decline from Georgia coast preagricultural to agricultural groups in cross-sectional areas and second moments of area of the femoral midshaft divided by bone length² (areas) or bone length⁴ (second moments of area) (see Fig. 1). Asterisks indicate statistical significance of t-tests between groups: *P < 0.05.

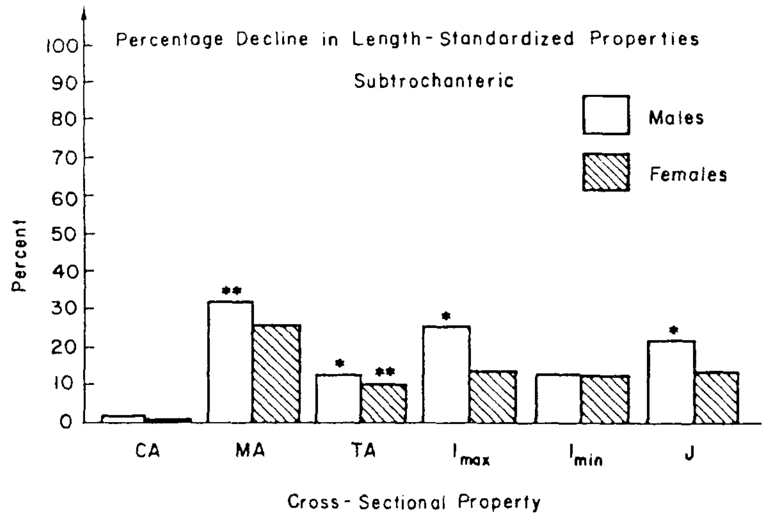

Fig. 4. Percentage decline from Georgia coast preagricultural to agricultural groups in cross-sectional areas and second moments of area of the femoral subtrochanteric section divided by bone length² (areas) or bone length⁴ (second moments of area) (see Fig. 1). Asterisks indicate statistical significance of t-tests between groups: *P < 0.05; **P < 0.01.

All of these changes in the distribution of bone tissue within cross sections strongly suggest a reduction in mechanical loading of the femur in the agricultural group. While a general decrease in skeletal size and cross-sectional area could be brought about by both nutritional and mechanical factors, it seems unlikely that a nutritional change (short of an obvious gross pathology such as rickets) would explain the redistribution of bone area within cross sections that was observed.

With regard to sex differences, the present study supports earlier observations of increased sexual dimorphism in body size (stature) in the agricultural group (Larsen, 1982). However, the present findings indicate no increase in sexual dimorphism in dimensions standardized by bone length (Table 2 and Figs. 3 and 4). Thus, *relative* to skeletal size or stature, the change in mechanical loadings of the femur appears to have been similar in males and females. This suggests that the greater reduction in body *size* among agricultural females may have been due principally to nutritional factors, an interpretation supported by other skeletal evidence cited above. Interestingly, certain cross-sectional shape changes, specifically greater circularity in the agricultural group, were more pronounced among males. This may indicate a greater reduction in particular *types* of mechanical loadings of the femur among males, i.e., A–P bending near midshaft and M–L bending in the proximal diaphysis (Ruff and Hayes, 1983a; also see below). The meaning of the increase in antetorsion of the femoral head and neck among agricultural females, and consequent change in orientation of the subtrochanteric section, is obscure at present, although it may indicate an alteration in loadings about the hip joint among females (Ruff and Hayes, 1983b).

In sum, our results indicate that the adoption of corn agriculture on the Georgia coast was very likely associated in both sexes with a decrease in mechanical stress, at least in the femur and probably in the lower limb as a whole. A possible concurrent decrease in nutritional status may have been more marked among females. This suggests that while changes in general activity level were about equal in both sexes, changes in diet were greater in females, possibly implying a greater dependence upon corn as a primary food source among agricultural females (Larsen, 1982).

The relative contributions of evolutionary (genetic) and secular (growth and development) effects in bringing about these structural changes cannot be definitely determined from the available evidence. However, the relatively short time period involved appears to argue for secular rather than evolutionary factors. All but two individuals in the preagricultural group postdate A.D. 500,

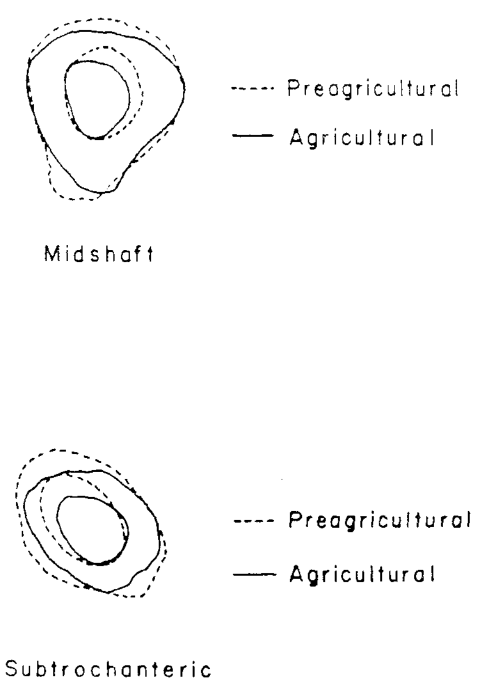

Fig. 5. Cross-sectional outlines of male Georgia coast preagricultural and agricultural femora, scaled for equal bone lengths.

thus, the maximum time difference between groups is about 1,000 years or 40 generations, and the mean difference about 500 years or 20 generations. While some changes in gene frequency could have occurred over this time span, it seems likely that most structural changes were due primarily to differential bone remodeling during growth and development.

Other studies

Many (but not all) investigators have reported a decline in stature with the transition to agriculture in various regional archaeological sequences (Angel, 1946, 1971, 1975; Stewart, 1949, 1953; Saul, 1972; Nickens, 1976; Cohen and Armelagos, in press). In most cases, the explanation given for such a decline has been primarily nutritional, i.e., a general decline in nutritional quality. An increase in circularity of femoral and tibial diaphyseal cross sections with the adoption or intensification of agriculture has also been reported for population samples from Point of Pines, Arizona (Bennett, 1973) and the Ohio River Valley (Perzigian et al., in press).

----- Preagricultural

—— Agricultural

---- Preagricultural

—— Agricultural

ric

ınal outlines of male Georgia coast
griculturaI femora, scaled for equal

um time difference between
1,000 years or 40 genera-
nean difference about 500
·ations. While some changes
·y could have occurred over
it seems likely that most
es were due primarily to dif-
nodeling during growth and

)ther studies

. all) investigators have re-
in stature with the transi-
ture in various regional
·quences (Angel, 1946, 1971,
949, 1953; Saul, 1972; Nick-
ı and Armelagos, in press).
e explanation given for such
·n primarily nutritional, i.e.,
e in nutritional quality. An
ılarity of femoral and tibial
; sections with the adoption
ı of agriculture has also been
·ulation samples from Point
ıa (Bennett, 1973) and the
·y (Perzigian et al., in press).

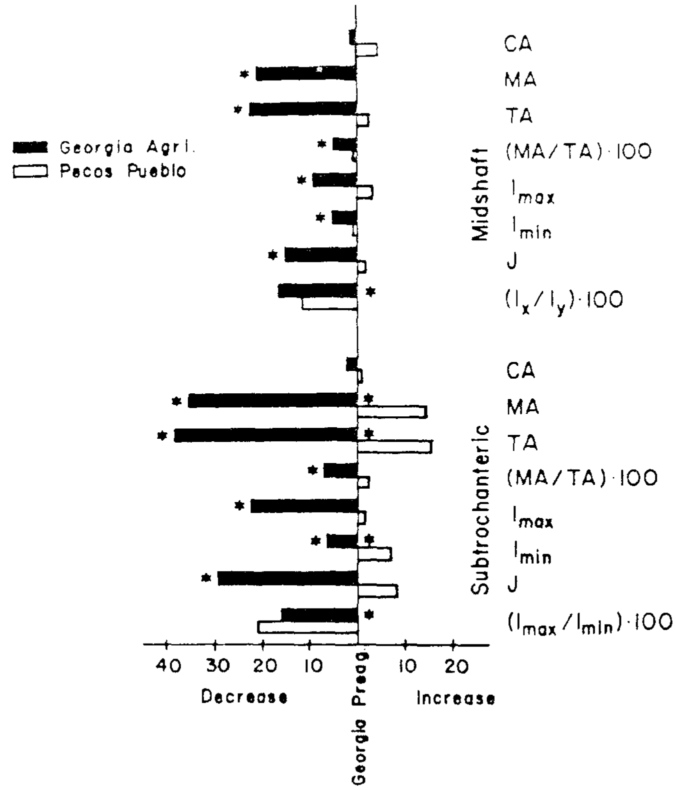

Fig. 6. Comparison of cross-sectional geometric properties of the femur in the Georgia coast preagricultural and Pecos Pueblo, New Mexico (Ruff and Hayes, 1983a) samples (see Abbreviations). Asterisks indicate statistically significant ($P < 0.05$) differences between the Pecos sample and one of the Georgia coast samples (left asterisk: Pecos—Georgia agricultural; right asterisk: Pecos—Georgia preagricultural). All data divided by bone length^2 (areas) or bone length^4 (second moments of area).

This latter change in cross-sectional shape is apparently part of a more general worldwide trend since the Upper Paleolithic (Buxton, 1938; Brothwell, 1972), and may indicate a general decline in A–P bending stress in the lower limb (Lovejoy et al., 1976; Ruff and Hayes, 1983a).

A comparison of the Georgia coast data with similar femoral geometric data from our recent study of the Pecos Pueblo, New Mexico, sample (Ruff and Hayes, 1983a,b) is shown in Figure 6. The Pecos sample dates from ca. A.D. 1300 to 1600, approximately the same time period as the Georgia coast agricultural sample, and also had an economy based primarily on corn agriculture. All the data in Figure 6 have been divided by powers of bone length', as described above, and are presented as differences between the Georgia preagricultural sample and the Georgia agricultural and Pecos samples.[1]

Because of the general similarity in time period and subsistence strategy, it might be expected that structural properties of Pecos femora would more closely resemble the Georgia agricultural rather than the preagricultural group. However, as shown in Figure 6, for most geometric properties this is not the case. Cross-sectional areas, second moments of area, and relative size of the med-

[1]Because the sex ratios in the Georgia coast samples are not 50/50, and males consistently show greater values for these properties than females (Table 1), a correction was applied to the Georgia values so that males and females are weighted equally in each group.

ullary cavity (MA/TA) are all more similar in the Georgia preagricultural and Pecos samples. All of these properties (except cortical area) are significantly different in the Pecos and Georgia agricultural groups, and in the three cases where Georgia preagricultural–Pecos differences reach statistical significance (subtrochanteric MA, TA, and I_{min}) Pecos differs in a direction *opposite* to that of the Georgia agricultural group, i.e., an increase rather than a decrease. These data indicate that Pecos femora were at least as strong or robust relative to their lengths as the preagricultural femora from Georgia, and significantly stronger than the Georgia agricultural femora.

The two structural characteristics of the femur that show greater similarity in the Pecos and Georgia agricultural groups are the I_x/I_y ratio in the midshaft section and the I_{max}/I_{min} ratio in the subtrochanteric section. These two "shape" indexes were chosen for comparison because they best illustrate structural adaptations to A–P bending loads in the middle diaphysis and M–L bending loads (more precisely bending loads in the antetorsion plane of the femoral head and neck) in the proximal diaphysis (Ruff and Hayes, 1983a,b). Lower indexes and thus greater circularity of cross sections at both locations are characteristic of the Pecos and Georgia agricultural samples compared to the Georgia preagricultural sample.

We have previously argued that cross-sectional shape changes of this type probably reflect at least partly changes in the *types* of mechanical loadings present, i.e., relative A–P and M–L loadings of the lower limb (Ruff and Hayes, 1983a,b). Thus, taken together, the present results indicate that the overall level of activity (at least that involving the lower limb) was more similar in the Georgia preagricultural and Pecos samples (and greater than in the Georgia agricultural group), but that the types of activities engaged in were more similar in the Georgia agricultural and Pecos groups.

It seems plausible that activity types would be more similar in two agricultural societies than in a hunting-gathering society. Relative reduction in A–P bending loads in the midshaft femur could be brought about by relatively less running and climbing and more walking (Ruff and Hayes, 1983b). A reduction in M–L bending loads in the proximal femur is more difficult to interpret precisely, but probably indicates a relative decrease in forces applied to the femoral head and moments generated about the hip joint due to action of the gluteal abductors (Rybicki et al., 1972). While changes in other types of activities could cause such a decrease, it is worth noting that peak joint reaction forces on the hip during stair climbing and rapid walking may reach values of more than seven times body weight, almost twice those incurred during normal level walking (Paul, 1967, 1976; Crowninshield et al., 1978). Abduction–adduction moments about the hip also increase greatly during stair climbing and descending (Andriacchi et al., 1980).

Thus, a possible scenario of less running and climbing, and more walking and possibly other more sedentary pursuits such as lifting and carrying in the two agricultural groups, is at least consistent with the available biomechanical data. The relatively more robust Pecos femora may indicate that while the basic types of activities were similar in the two agricultural groups, they were more difficult and mechanically demanding at Pecos than on the Georgia coast, an interpretation which seems reasonable in light of the general differences in environment in the two regions (Kidder, 1924, 1932, 1958; Thomas et al., 1978). It is also interesting that the sex difference in cross-sectional shape of the femur described previously for Pecos (Ruff and Hayes, 1983b), namely, a more A–P areal distribution of bone in males, is also present in both Georgia coast samples (Table 1). This may be at least partly accounted for by a sexual division of labor, with males doing more hunting and females more gathering and, later, crop cultivating, which was characteristic of both the Georgia coast region as well as Pecos Pueblo (Larsen, 1982; Ruff and Hayes, 1983b). The fact that femoral cross-sectional shape of Georgia coast males changed more than females with the transition to agriculture would seem to indicate a greater change in the type of activities (but not level of activity) among males. Unfortunately, the available archaeological and ethnohistoric data for this region are too sparse to allow further examination of this possibility.

These interpretations are not meant to imply that activity differences were the only factors involved in the observed structural differences between Pecos and Georgia coast femora. Nutritional differences must certainly also have been important, and may, for example, partly explain why Pecos Pueblo

the femoral head and mo-
about the hip joint due to
ıteal abductors (Rybicki et
changes in other types of
:ause such a decrease, it is
ıt peak joint reaction forces
g stair climbing and rapid
:h values of more than seven
;ht, almost twice those in-
ormal level walking (Paul,
·nninshield et al., 1978). Ab-
ın moments about the hip
eatly during stair climbing
Andriacchi et al., 1980).
le scenario of less running
ıd more walking and possi-
sedentary pursuits such as
ing in the two agricultural
st consistent with the avail-
:al data. The relatively more
ora may indicate that while
of activities were similar in
ıral groups, they were more
:hanically demanding at Pe-
Georgia coast, an interpreta-
s reasonable in light of the
es in environment in the two
1924, 1932, 1958; Thomas et
ılso interesting that the sex
ss-sectional shape of the fe-
eviously for Pecos (Ruff and
namely, a more A–P areal
one in males, is also present
coast samples (Table 1). This
; partly accounted for by a
of labor, with males doing
nd females more gathering
cultivating, which was char-
ı the Georgia coast region as
ıeblo (Larsen, 1982; Ruff and
The fact that femoral cross-
: of Georgia coast males
ıan females with the transi-
ıre would seem to indicate a
in the type of activities (but
vity) among males. Unfortu-
lable archaeological and eth-
for this region are too sparse
: examination of this possi-

:tations are not meant to im-
y differences were the only
l in the observed structural
een Pecos and Georgia coast
ional differences must cer-
e been important, and may,
tly explain why Pecos Pueblo inhabitants were shorter than either Georgia coast sample (femoral length averages 8% shorter than Georgia preagricultural and 2% shorter than Georgia agricultural). However, it is interesting that in all three samples the area of bone (CA) standardized for bone length differences is almost identical (Fig. 6). Again, as with comparisons within the Georgia coast, it is only the *distribution* of bone area which differs. This kind of structural difference seems to suggest localized (mechanical) rather than systemic (nutritional or other) effects.

While much of the foregoing discussion is speculative, it does serve to illustrate how various hypotheses regarding activity and lifestyle changes can begin to be formulated and tested using biomechanical techniques applied to archaeological material. It also may serve as a caution against overemphasis of purely nutritional factors in explaining changes in body form concurrent with subsistence strategy changes. Increases or decreases in overall body size are probably strongly related to nutrition (Guzman, 1968). However, localized remodeling or shape changes in the skeleton are probably best explained as adaptations to altered mechanical loadings. Our data indicate that the adoption of agriculture and a more sedentary lifestyle on the Georgia coast was associated with a decrease in overall mechanical stress, and possibly a change in the types of mechanical stress in the femur, at least among males. Further studies will show how general these changes were, and how limited to the lower limb.

ACKNOWLEDGMENTS

This work was supported in part by National Institutes of Health (NIH) Traineeship AM 07112 (CBR); the Edward John Noble Foundation, the St. Catherines Island Foundation, and the American Museum of Natural History (CSL); and NIH grants AM 26740 and AM RCDA 00749 (WCH). We would like to thank Dr. D. Ubelaker for permission to use skeletal material from the Smithsonian Institution. A preliminary version of this paper was presented at the 1983 annual meeting of the American Association of Physical Anthropologists.

LITERATURE CITED

Andriacchi, TP, Andersson, BJ, Fermier, RW, Stern, D, and Galante, JO (1980) A study of lower-limb mechanics during stair climbing. J Bone Joint Surg. *62A*:749–757.

Angel JL (1946) Skeletal changes in ancient Greece. Am. J. Phys. Anthropol.. *41*:69–97.

Angel, JL (1971) The People of Lerna: Analysis of a Prehistoric Aegean Population. Washington, DC: Smithsonian Institute Press.

Angel, JL (1975) Paleoecology, paleodemography, and health. In S Polgar (ed): Population, Ecology and Social Evolution. The Hague: Mouton, pp. 167–190.

Bennett, KA (1973) The Indians of Point of Pines, Arizona: a comparative study of their physical characteristics. Anthropol Papers Univ. Ariz., no. 23.

Brothwell, DR (1972) Digging Up Bones. London: British Museum of Natural History.

Brues, A (1959) The spearman and the archer—an essay on selection in body build. Am. Anthropol. *61*:457–469.

Buxton, LHD (1938) Platymeria and platycnemia. J. Anat. *73*:31–36.

Cohen, MN, and Armelagos, GJ Paleopathology at the Origins of Agriculture. New York: Academic Press (in press).

Crowninshield, RD, Johnston, RC, Andrews, JG, and Brand, RA (1978) A biomechanical investigation of the human hip. J. Biomech. *11*:75–85.

DePratter, CB (1977) Environmental changes on the Georgia coast during the prehistoric period. Early Georgia *5*:1–14.

Frayer, DW (1981) Body size, weapon use, and natural selection in the European Upper Paleolithic and Mesolithic. Am. Anthropol. *83*:57–73.

Guzman, MA (1968) Impaired physical growth and maturation in malnourished populations. In NS Schrimshaw and JE Gordon (eds): Malnutrition, Learning and Behavior. Cambridge, MA: MIT Press, pp. 42–54.

Kidder, AV (1924) An introduction to the study of southwestern archaeology with a preliminary account of the excavations at Pecos. Pap. Phillips Acad. SW Exped., no. 1, New Haven, CT: Yale University Press.

Kidder, AV (1932) The artifacts of Pecos. Pap. Phillips Acad. SW Exped., no. 6. New Haven, CT: Yale University Press.

Kidder AV (1958) Pecos, New Mexico: Archaeological notes. Pap. Peabody Found. Arch., Vol. 5. Andover, MA: Phillips Academy.

Larsen, CS (1981) Functional implications of postcranial size reduction on the prehistoric Georgia coast, U.S.A. J. Hum. Evol. *10*:489–502.

Larsen, CS (1982) The anthropology of St. Catherines Island. 3. Prehistoric human biological adaptation. Anthrop. Papers Am. Mus. Nat. Hist. *57*(3):159–270.

Larsen, CS (1983a) Behavioural implications of temporal change in cariogenesis. J. Archaeol. Sci. *10*:1–8.

Larsen, CS (1983b) Subsistence role behavior and the infectious disease experience on the prehistoric Georgia coast. Am. J. Phys. Anthropol. *60*:216.

Lovejoy, CO, Burstein, AH, and Heiple, KG (1976) The biomechanical analysis of bone strength: a method and its application to playcnemia. Am. J. Phys. Anthropol. *44*:489–506.

Nagurka, ML, and Hayes, WC (1980) An interactive graphics package for calculating cross-sectional properties of complex shapes. J. Biomech. *13*:59–64.

Nickens, PR (1976) Stature reduction as an adaptive response to food production in Mesoamerica. J. Archaeol. Sci. *3*:31–41.

Paul, JP (1967) Forces transmitted by joints in the human body. Proc. Inst. Mech. Eng. *181*(3J):8–15.

Paul, JP (1976) Approaches to design: Force actions transmitted by joints in the human body. Proc. R. Soc.

Lond. *B192*:163–172.

Perzigian, AJ, Tench, PA. and Braun, DJ Prehistoric health in the Ohio River Valley. In MN Cohen and GJ Armelagos (eds): Paleopathology at the Origins of Agriculture. New York: Academic Press (in press).

Ruff, CB (1981) Structural changes in the lower limb bones with aging at Pecos Pueblo. Ph.D. thesis, University of Pennsylvania.

Ruff, CB, and Hayes, WC (1983a) Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation. I. Method and general patterns of variation. Am. J. Phys. Anthropol. *60*:359–381.

Ruff, CB, and Hayes, WC (1983b) Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation. II. Sex, age, and side differences. Am. J. Phys. Anthropol. *60*:383–400.

Rybicki, EG, Simonen, FA, and Weis, EB (1972) On the mathematical analysis of stress in the human femur. J. Biomech. *5*:203–215.

Saul, F (1972) The human skeletal remains at Altar de Sacrificos: an osteobiographic analysis. Papers Peabody Mus. Archaeol. Ethnol., Vol. 63, no. 2. Cambridge, MA: Harvard University.

Stewart, TD (1949) Notas sobre esqueletos humanos prehistoricos hallados en Guatemala. Anthropol. Hist. Guatemala *1*:23–24.

Stewart, TD (1953) Skeletal remains in Zaculeu, Guatemala. In RF Woodbury and AS Trik (eds): The Ruins of Zaculeu, Guatemala. Boston, MA: United Fruit Co.

Thomas, DH, Jones, GD, Durham, RS, Larsen CS (1978) The anthropology of St. Catherines Island: 1. Natural and cultural history. Anthropol. Papers Am. Mus. Nat. Hist. *55*:155–248.

Thomas, DH, and Larsen, CS (1979) The anthropology of St. Catherines Island: 2. The Refuse-Deptford mortuary complex. Anthropol. Papers Am. Mus. Nat. Hist. *56*:1–180.