

# Biomechanical Analysis of Humeral and Femoral Structural Variation in the Great Plains

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*Variation in humeral and femoral structural morphology of Great Plains populations is examined for differences due to subsistence practice and geographical location. The sample consists of Archaic hunter-gatherers, early and middle Woodland hunter-gatherers, late Woodland incipient horticulturalists, Plains Village horticulturalists, and equestrian nomads from the northern, central, and southern Plains. In general, skeletal morphology on the Plains is relatively homogeneous throughout time and space. There are few significant univariate differences in same sex comparisons or in sexual dimorphism due to either subsistence practice or geographical region. However, males tend to cluster partially by subsistence practice, while females cluster by geographical region. Subsistence differences are generally associated with long bone size and activity related robusticity. Geographical variation between groups is most likely associated with climatically-induced differences in body build and not terrain relief.*

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Employing knowledge about the interrelationships between bone function and morphology, physical anthropologists have commonly used long bone biomechanical properties to infer behavior or activity patterns, especially levels of mobility and workload, for archaeologically derived populations (see overviews in Bridges 1995; Larsen 1997; Ruff 2000a). Ruff et al. (2006:484) have argued that “while physical context and material culture give clues to past behavior, analysis of skeletons themselves is the most direct way to reconstruct individual behavior, and to explore intra- and interpopulational differences in behavior.” However, despite the extensive use of biomechanical studies by physical anthropologists to reconstruct the activity patterns of prehistoric and historic Native American populations, only a few studies (Cole 1994; Ruff 1994; Wescott and Cunningham 2006) have examined populations from the Great Plains using this approach. Furthermore, these reports were primarily restricted to the analysis of skeletal remains from the northern Plains.

This study expands on previous research of Great Plains populations by employing a significantly larger and more geographically and temporally diverse sample, and examining both upper and lower limb bone morphology. Its goals are to investigate variation in structural morphology of the humerus and femur as related to differences in subsistence strategy and geographical location. To achieve these goals, humeral and femoral dimensions and structural variables from Great Plains populations are examined within an archaeological and historical framework using a biomechanical approach.

## BIOMECHANICAL ANALYSIS

Bone morphology is determined by the interaction of numerous factors (e.g., genetics, hormones, health, and mechanical load), but researchers have demonstrated that a bone’s architecture is adapted during life to meet activity-related mechanical demands placed on it (Frost 1987, 1988; Lanyon et al. 1982; Martin et al. 1998). In biome-

chanical studies, cross-sectional geometric properties (subperiosteal area, cortical bone area, and second moments of area) of long bones are used to estimate the strength (ability to resist mechanical forces) of the bone under particular mechanical loads. The primary loading forces acting on bone are tension, compression, shear, bending, and torsion. In response to these mechanical forces, the physiological processes of bone modeling shape and sculpt the diaphyseal cross section of long bones during life so that the bone's diameter, cross-sectional shape, and cortical thickness reflect the manner and magnitude of the mechanical forces that were placed on the bone (Larsen 1997; Ruff 2000a). The primary task of bone modeling is the sizing and shaping of bones so that their typical peak mechanical loads caused by normal daily activities do not produce dynamic or static strains great enough to cause bone failure (Frost 1985).

Most biomechanical studies of Native American long bones have focused on changes during the transition from hunting-gathering to horticulture. In most geographical regions, hunter-gatherers, especially males, have stronger bones, more pronounced upper limb bone bilateral asymmetry, and less circular femoral midshaft cross sections compared to horticulturalists (Larsen 1997; Ruff 1987, 2000a). There is also usually greater sexual dimorphism, especially in femoral midshaft shape, among hunter-gatherers than horticulturalists (Ruff 1987; Wescott 2006a). Many researchers have concluded that subsistence-dependent levels of terrestrial logistic mobility and workload are the primary causes for the variation in long bone structural properties between hunter-gatherers and horticulturalists when differences in body size are controlled (Bridges 1989, 1995; Larsen 1997; Ruff 1987, 2000a).

Researchers (e.g., Holt 2003; Larsen 1997; Ruff 1987, 2000a; Stock 2006; Stock and Pfeiffer 2001, 2004;) who contend there is a strong relationship between lower limb bone structure and mobility have argued that activities such as running cause greater anteroposterior (AP) than mediolateral (ML) bending loads on the femur and tibia diaphyses. As a result, more bone is laid down in the AP than ML plane of the diaphyseal cross

section during modeling. The effect is that highly mobile groups, especially males in these groups, have greater AP than ML cross-sectional dimensions (greater AP/ML ratio) and greater AP bending strength. Since males tend to be more mobile than females in hunter-gatherer populations, the level of sexual dimorphism in femoral midshaft shape is also greater in mobile hunter-gatherer groups compared to relatively sedentary horticultural groups (Larsen 1995, 1997; Ruff 1987, 2000a).

Several researchers have also argued that work load intensity associated with subsistence activities can explain many of the differences in humeral and femoral cross-sectional properties between hunter-gatherers and horticulturalists. Bridges (1989) found that in the American Southeast, long bone (humerus and femur) strength increased in both males and females, but especially humeral strength in females, during the transition from hunting-gathering to agriculture. She attributed the increased strength to the greater intensity of work needed to produce, harvest, and process crops by horticulturalists compared to subsistence activities performed by hunter-gatherers. Later, Bridges et al. (2000) observed that humeral strength increased significantly at the beginning of the transition from hunting-gathering to agriculture in the Southeast when native seed crops were primarily being grown, but decreased again with the introduction of maize. They argued that native seed crops were relatively harder to process than maize and therefore required more intense upper body labor (Bridges et al. 2000). Likewise, Larsen and Ruff (1994) discovered that long bone strength among Native Americans from Florida increased after Spanish contact, which they ascribed to an increase in the overall workload among these populations living in Spanish missions. Wescott and Cunningham (2006) also found that long bone strength and asymmetry increased among Arikara females as they began to intensify crop production to have surplus vegetables for trade. Finally, Wescott (2001) found that long bone strength corresponded to workload intensity more than to mobility or terrain type among a diverse sample of Native Americans.

In addition to comparing differences in long

bone structure between hunter-gatherers and horticulturalists, several biomechanical studies have examined the effects of ecological factors, terrain relief and ambient temperature, on long bone morphology. Ruff (1999) observed that groups living in rugged mountainous terrains, regardless of subsistence strategy, have stronger lower limb bones than groups living in less rugged terrains (coastal regions and Great Plains). He (Ruff 1999, 2000a) argues that while lower limb morphology may correspond to subsistence activities, terrain relief could have a greater influence on lower limb robusticity. Stock (2006) found that long bone robusticity correlates negatively with temperature, and Pearson (2000) revealed that the long bones from populations in cold environments are generally more robust than those from populations in warm climates. The primary reason for these findings is that climate affects limb length, and therefore robusticity, when it is expressed in terms of diaphyseal diameter or strength relative to length. Interestingly, Pearson (2000) also observed that hunter-gatherers tend to be more robust than agriculturalists in cold climates, while the pattern is reversed in warm climates. Regarding shape, Weaver (2003) discovered that populations in cold climates have more circular femoral midshafts compared to populations in warm climates. Again, these findings primarily reflect climatically induced body shape differences that influence mediolateral mechanical loading on the bone resulting in more circular diaphyses in cold climates.

These biomechanical studies have shown that factors affecting long bone morphology are dependent on local ecological circumstances, and that there are regional differences in how changes in activities and workload associated with the transition from hunting-gathering to horticulture affect long bone morphology. Together, these studies emphasize the need to evaluate populations from the Great Plains, taking into consideration the distinct culture and ecology of the Plains. The Great Plains is unique in its geology, climate, and biodiversity, and the peoples of the Plains developed remarkable and unparalleled ways of adapting to this biophysical environment. As a result, the long bone morphology of Plains Native Americans is also likely unique.

### PREVIOUS BIOMECHANICAL STUDIES OF GREAT PLAINS SKELETONS

While numerous biomechanical studies have been conducted to help interpret behavior among prehistoric and historic Native American groups, only three previously published studies (Cole 1994; Ruff 1994; Wescott and Cunningham 2006) have focused on Great Plains skeletal remains using a biomechanical approach. Cole (1994) uses femur and tibia external measurements from Woodland, Middle Missouri, and Coalescent tradition samples to examine long bone structural changes associated with the transition from hunting-gathering to horticulture in the northern Plains. He found that with the shift from hunting-gathering to horticulture there were no significant changes in same-sex bone size or in the degree of sexual dimorphism, but that Coalescent males had significantly more AP elongated (greater AP/ML ratio) femoral midshafts than earlier Woodland groups. Cole (1994) suggests that dietary and activity-related stresses associated with the transition from hunting-gathering to horticulture in the northern Plains may not have been great enough to cause significant changes in bone size. However, he argues that the greater femoral midshaft AP/ML ratio in Coalescent males compared to earlier Woodland groups could be interpreted as relatively greater mobility among Coalescent compared to earlier Woodland groups.

Ruff (1994) examined femur midshaft cross-sectional morphology in a sample composed of Woodland, Middle Missouri, and Postcontact Coalescent populations from the northern Plains and Washita River phase populations from the southern Plains. In his comparison of cultural-temporal groups, Ruff (1994) found significant group differences in femur midshaft shape for both males and females, but not in torsional or bending strength. He also observes that sexual dimorphism in femur midshaft cross-sectional cortical area, torsional strength, and shape declined with time in the Great Plains. The most interesting result of Ruff's (1994) study is that southern Plains horticulturalists had significantly more AP elongated (greater AP/ML ratio) femoral midshafts compared to northern Plains horticulturalists de-

spite any strong archaeological evidence for differences in subsistence practices between these two groups. Ruff (1994) argues that horticulturalists of both sexes in the southern Plains were highly mobile compared to horticulturalists in the northern Plains. However, Ruff's (1994) southern Plains sample consisted of only 5 males and 13 females, so, as he notes, the results could be due to sampling error.

Wescott and Cunningham (2006) examined temporal changes in Arikara humeral and femoral cross-sectional architecture. They observed significant changes in femoral and humeral cross-sectional asymmetry among females through time, which they attribute to increased workloads necessary to produce surplus crops for trade. Significant temporal variation in Arikara males was restricted to the humerus, with asymmetry increasing through time. Wescott and Cunningham (2006) suggest that a greater reliance on firearms over bows through time might explain this observation. They also observe that the pattern of sexual dimorphism changed through time in the Arikara, but they argue that the changes were probably due to a combination of dietary and mechanical factors.

In general, biomechanical studies of long bones from the Plains have raised more questions than they have answered. As Owsley and Jantz (1999) point out, there is a need to evaluate hypotheses concerning the relationship between subsistence strategies and variation in long bone size, robusticity, and sexual dimorphism among Great Plains populations. Furthermore, Ruff (1994) argues that a study including larger samples and

structural properties of both the upper and lower limbs is needed to understand the patterns of long bone variation in the Great Plains. This study undertakes these goals and attempts to fill in some of the gaps in our knowledge of Plains postcranial variation.

## MATERIALS AND METHODS

### Samples

Adult humeri and femora (N = 1,198 individuals) from Great Plains archaeological sites representing five subsistence groups and three geographical regions are used in this study (Table 1). Subsistence groups include Archaic broad-spectrum hunter-gatherers (BHG), Early and Middle Woodland hunter-gatherers (WHG), Late Woodland incipient horticulturalists (WIH), Plains Village horticulturalists-hunters (VHH), and equestrian hunter-gatherers (EHG). This last sample is represented by historic Blackfoot, Cheyenne, Comanche, Crow, and Sioux. Geographically, the sample was divided into northern, central, and southern Great Plains groups. Sex and age were estimated for each individual using standard osteological methods (Bass 1995; Buikstra and Ubelaker 1994).

### Data Collection

Long bone cross-sectional properties can be obtained two ways: 1) using a variety of invasive and non-invasive cross-sectional methods (direct sectioning or cutting the bone, computed tomography (CT) imaging, or biplanar radiography methods; see O'Neill and Ruff 2004 for an overview of these methods) or 2) by estimating the cross-

**Table 1. Subdivisions of Sample by Subsistence Strategy and Geographical Location.**

Class Variable	Abbreviation	N <sup>a</sup>	Description
<u>Subsistence Strategies (N=1118)</u>			
Broad-Spectrum Hunter-Gatherer	BHG	28	Archaic
Woodland Hunter-Gatherer	WHG	43	Early and Middle Woodland
Woodland Incipient Horticulturalist	WIH	44	Late Woodland
Village Horticulturalist-Hunter	VHH	942	Plains Villagers
Equestrian Hunter-Gatherer	EHG	61	Historic Equestrian Nomads
<u>Geographical Region (N=1198)</u>			
Northern Plains (NP)	NP	831	North of Nebraska/South Dakota border
Central Plains (CP)	CP	235	Northern Plains border to Arkansas River
Southern Plains (SP)	SP	132	South of Arkansas River

<sup>a</sup> Maximum number of individuals

sectional parameters using external measurements (Pearson 2000; Rockhold 1998; Ruff 1987; Wescott 2001, 2006a). There are advantages and disadvantages to both methods. The advantage of using cross-sectional methods is that they provide information about not only the size and shape of the bone but also its internal architecture (cortical bone thickness and medullary cavity shape). However, cross-sectional methods require substantial time, special facilities, and considerable cost. Furthermore, direct sectioning of the bones is rarely permitted. External measurements, on the other hand, can be collected relatively quickly, with minimal equipment, and at relatively little expense. As a result, much larger samples can be collected, but information about the internal architecture of the bone is lost. However, Jungers and Minns (1979), Pearson (2000), Rockhold (1998), and Wescott (2001) have demonstrated that most long bone cross-sectional properties can be estimated with validity using external dimensions. Therefore external measurements can be used as a substitute for cross-sectional properties in biomechanical studies, but the results should be interpreted more cautiously (see Wescott 2006a for discussion). In this study, external dimensions are used to estimate cross-sectional properties. Since a comparison of multiple subsistence groups from three geographical regions of the Plains requires an extremely large sample size, the use of external dimensions to estimate cross-sectional properties is preferred even though some structural information is lost.

Ten external measurements (Table 2) of humeri and femora were obtained from the University of Tennessee/Smithsonian Institution (UT/SI) database (Wescott 2001). These measurements provide information about the length, diaphyseal diameters, and head breadth of the bones. Left bones were preferentially used but right bones were used if the left side was damaged or missing. Only mature bones (epiphyses closed) with no observable evidence of infection or fractures were used. The UT/SI database is composed of skeletal data collected by multiple observers, so noise in the data resulting from interobserver error is possible. However, the majority of the data were collected by Dr. Owsley (Smithsonian Institution), Dr. Jantz (University of Tennessee), or

**Table 2. Long Bone Dimensions.**

Bone	Measurement <sup>a</sup>	Abbrev.
Humerus	Maximum length	HML
	Head diameter	HHD
	Maximum midshaft diameter	MDS
	Minimum midshaft diameter	MDM
Femur	Maximum length	FML
	Head diameter	FHD
	AP subtrochanteric diameter	APD
	ML subtrochanteric diameter	MLD
	AP midshaft diameter	APS
	ML midshaft diameter	MLS

<sup>a</sup>See description of measurements in Wescott (2001)

personnel trained by them, so interobserver error is minimized. See Adams and Byrd (2002) and Wescott (2005) for a complete discussion of interobserver error in long bone measurements.

### Derived Structural Properties

Structural variables were calculated using the external dimensions taken at midshaft for humeri and at subtrochanteric and midshaft for femora (Table 3). These variables approximately reflect the cross-sectional properties of the bone at each location (Cole 1994; Larsen 1997; Ruff 1987). The diaphyseal locations were selected because they are biomechanically important and frequently used by other researchers in biomechanical studies.

A shape index, defined as the ratio of the AP diameter to the ML diameter of the bone shaft (Cole 1994; Larsen 1997; Ruff 1987), was calculated at each level for the femur (Table 3; FSS, FMS). Similarly, a ratio of the maximum diameter to the minimum diameter was calculated at midshaft for the humerus (Table 3; HMS). The shape index provides an estimate of the  $I_{AP}/I_{ML}$  ratio (AP second moments of area divided by ML second moments of area) obtained from diaphyseal cross sections (Rockhold 1998; Ruff 1987; Wescott 2001). A femoral shape index of 1.0 indicates the diaphysis is circular and equally resistant to bending in the AP and ML planes. A shape index greater than 1.0 indicates that the diaphyseal cross section is larger and relatively more resistant to bending forces in the AP plane compared to the ML plane. If the shape index is less than one, the diaphysis is wider in the ML plane

**Table 3. Structural Properties Determined for the Humerus and Femur.**

Bone	Property	Abbrev.	Formula
Humerus	Midshaft shape	HMS	MDS/MDM
	Midshaft robusticity	HMR	$100 * (\sqrt{MDS * MDM}) / HHD$
	Midshaft area	HMA	$\pi * (MDS/2) * (MDM/2) / HML^{3*10^8}$
Femur	Subtrochanteric shape	FSS	APD/MLD
	Subtrochanteric robusticity	FSR	$100 * (\sqrt{APD * MLD}) / FHD$
	Subtrochanteric Polar SMA <sup>a,b</sup>	FSJ	$100 * (-124812 + 2925 * APD + 3360 * MLD) / (BM * FML)$
	Subtrochanteric area <sup>b</sup>	FSA	$100 * (\pi * (APD/2) * (MLD/2) / BM)$
	Midshaft shape	FMS	APS/MLS
	Midshaft robusticity	FMR	$100 * (\sqrt{APS * MLS}) / FHD$
	Midshaft Polar SMA <sup>a,b</sup>	FMJ	$100 * (-102286 + 2721 * APS + 2697 * MLS) / (BM * FML)$
Midshaft area <sup>b</sup>	FMA	$100 * (\pi * (APS/2) * (MLS/2) / BM)$	

<sup>a</sup>SMA = second moment of area

<sup>b</sup>BM = body mass calculated from FHD following Ruff et al. (1991)

than the AP plane (Larsen, 1997). For the humerus, an index of 1.0 indicates the minimum and maximum values are equal.

Robusticity, which provides an estimate of general bone strength, was calculated at each diaphyseal level. The term “robusticity” is commonly used in the anthropological literature, but as Pearson (2000) has pointed out, there are numerous definitions. Traditionally, long bone robusticity is defined as diaphyseal thickness relative to bone length (Martin and Saller 1957), but it has also been applied to joint surface size, bending strength, torsional strength, and cortical area relative to bone length (Pearson 2000). In most biomechanical studies, robusticity is defined as bone strength (estimated using the polar second moment of area [J]) relative to body mass or a proxy for body mass (Ruff et al. 1993). Skeletal robusticity is highly correlated with body mass, and several researchers (e.g., Holiday 2002; Ruff 2000b) have argued that it is vital to standardize robusticity by body mass so that behaviorally induced morphology can be observed. In this study, robusticity was calculated as diaphyseal size relative to head diameter using the equations in Table 3 (HMR, FSR, and FMR) because femur head size is more highly correlated with body mass than is bone length (Lieberman et al. 2001; Ruff et al. 1991), and is a more appropriate measure to control for body mass differences.

An estimation of the polar second moment of area (J) was also calculated for each diaphyseal level of the femur to provide a second estimation of robusticity (Table 3; FSJ, FMJ). The polar second moments of area provide an estimate of the bone’s resistance to twisting stress, and Lieberman et al. (2004) argue that J is the best single parameter to use in biomechanical studies. In this study, AP and ML dimensions (APS and MLS for the femur subtrochanter and APD and MLD for the femur midshaft) are used to predict J at each level on the femoral diaphyses using equations derived by Wescott (2001). This measure of robusticity could not be evaluated for the humerus because appropriate equations are not available. Wescott (2001) uses least squared regression to examine the relationship between external dimensions and cross-sectional properties obtained from CT images of Arikara femora. His results show that approximately 83 percent of the variation in J can be captured using external dimensions. In this study, the product of body mass and bone length is used to standardize J for differences in body size (Ruff 2000b). Body mass is estimated using the combined sex equation in Ruff et al. (1991).

Subperiosteal or total area, which measures diaphyseal size, was calculated using an elliptical formula at each diaphyseal level of the humerus and femur (Table 3; HMA, FSA, FMA). In this

method, an elliptical cross-sectional shape of the long bone is assumed, which means that only two dimensions (AP and ML diameter) are needed. A strong correlation exists between cross-sectional geometric values calculated using an elliptical formula and values obtained from actual cross sections of the same bone (Fresia et al. 1990; Ruff and Jones 1981). Subperiosteal area is standardized for differences in body size by dividing the area of the femur by body mass estimated from FHD (Auerbach and Ruff 2004; Ruff et al. 1991). Since the relationship between body mass and humeral area is unclear, humeral length to the third power is used as a proxy for body size (Ruff 2000a).

### Data Analysis

All statistical analyses were performed using SAS 9.1 software. Group comparisons were performed using analysis of variance (ANOVA) and multivariate canonical discriminant function analysis. The ANOVA procedure tests the null hypothesis that there are no differences between groups by evaluating if the variation in groups is larger than expected. Structural properties were used as dependent variables. When more than two groups are compared using ANOVA, it is necessary to use post hoc multiple comparison tests to determine which groups differ significantly and to control for Type 1 error (incorrectly rejecting the null hypothesis). Multivariate canonical discriminant analysis produces a linear combination of quantitative variables that maximizes between group variation. Plots of the first two canonical correlations allow for easy visualization of group similarities and differences.

## RESULTS

### Subsistence Strategy

#### Same-Sex Comparisons

Summary statistics for structural properties and selected measurements are provided in Table 4 by sex and subsistence strategy. Same-sex subsistence group comparisons for males and females are presented in Table 5 and Table 6, respectively.

Analysis of variance results for males indicate significant differences between subsistence groups in 10 variables, but only HHD, HMA, and FMS were significant in multiple comparison tests

(Table 5). The lack of statistical significance between groups in multiple comparison tests, especially with BHG, may be associated with the fact that cell sizes are not equal. For HHD and HMA, equestrian hunter-gatherers have the largest means and differ significantly from one or more of the other groups. Village horticulturalists (VHH) differ significantly from WIH in FMS. The early hunter-gatherers (WHG and BHG) have weaker femora at both subtrochanteric (FSR and FSJ) and midshaft (FMR and FMJ) compared to later horticulturalists and equestrians, but the difference does not reach significance in multiple comparison tests. Again, this may be due to small sample sizes in the early hunter-gatherers.

Even though males only differ significantly in a few variables by subsistence, multivariate analysis shows that males group based partially on subsistence and partially on temporal similarities (Figure 1). For the humerus (Figure 1A), the first canonical correlation (CAN 1: correlation = 0.26,  $p < 0.0001$ ) separates the horticulturalists (VHH and WIH) from the hunter-gatherers (BHG, WHG, EHG), and reflects primarily differences in size. Groups with high scores have larger humeral head diameters and greater midshaft areas. Differences in HHD and HMA also cause some dispersion of the hunter-gatherer males. The second canonical correlation (CAN 2: correlation = 0.18,  $p = 0.03$ ) further separates the three hunter-gatherer groups and the two horticulturalist groups as well as the more contemporaneous EHG and VHH from the earlier populations. Groups with high scores on this axis have a smaller humerus midshaft min/max ratio and are less robust at midshaft. The pattern of relationship is similar for the femur (Figure 1B) except the WIH cluster with the hunter-gatherers on CAN 1 (correlation = 0.33,  $p < 0.0001$ ) and the VHH and EHG on CAN 2 (correlation = 0.18,  $p < 0.0001$ ). The WIH and hunter-gatherers are less platymeric (smaller FSS) (CAN 1) than the VHH. Variation in CAN 2 primarily reflects a temporal pattern with femur midshaft area and robusticity increasing though time. However, the low canonical correlations for both the humerus and femur suggest that there is much greater within group variation than between group variation.

Significant differences were found among

Table 4. Summary Statistics by Subsistence Strategy and Sex.

Variable <sup>a</sup>	Statistic	BHG		WHG		WIH		VHH		EHG	
		F	M	F	M	F	M	F	M	F	M
HML	N	6	9	15	19	14	22	378	426	29	27
	Mean	300.3	319.7	301.8	327.4	302.4	326.6	299.3	320.8	310.4	324.4
	SD	14.0	17.4	16.3	12.9	16.5	15.7	13.5	14.3	17.8	25.9
HHD	N	6	10	14	25	16	21	373	428	28	27
	Mean	39.0	45.3	42.6	46.8	40.0	45.5	41.0	46.2	43.1	47.9
	SD	1.4	2.7	2.3	2.9	1.9	2.6	2.2	2.4	2.4	2.3
HMS	N	11	17	17	26	17	25	410	456	28	28
	Mean	1.47	1.44	1.40	1.36	1.44	1.42	1.39	1.36	1.41	1.38
	SD	0.2	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
HMR	N	6	10	14	22	16	21	372	425	27	27
	Mean	42.3	41.5	41.3	42.2	42.7	41.8	42.7	40.8	43.7	41.7
	SD	3.0	3.6	2.6	3.3	2.6	3.0	3.1	3.3	3.6	3.4
HMA	N	6	9	15	19	14	22	376	424	28	27
	Mean	795.7	865.9	903.1	887.6	833.3	825.3	904.6	853.5	942.8	971.6
	SD	122.6	182.8	194.0	119.6	111.2	118.3	155.4	157.0	209.7	450.9
FML	N	5	3	8	18	19	21	442	522	32	29
	Mean	415.6	444.3	423.7	450.6	421.2	451.8	415.5	449.4	436.1	439.2
	SD	18.1	26.9	24.1	19.1	24.5	20.8	19.6	19.6	22.9	17.7
FHD	N	4	1	7	18	19	19	420	507	29	29
	Mean	41.2	47.0	42.3	47.2	41.2	46.7	42.3	47.1	43.9	48.1
	SD	1.5	—	1.8	1.7	2.3	1.8	2.1	2.3	2.7	2.6
FSS	N	4	3	6	13	18	18	431	508	29	28
	Mean	0.70	0.83	0.76	0.81	0.75	0.83	0.75	0.77	0.79	0.82
	SD	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
FSR	N	4	1	5	13	18	16	409	494	26	28
	Mean	59.7	61.5	61.0	61.7	66.6	65.2	63.8	63.4	64.5	64.5
	SD	1.7	—	5.0	4.1	3.9	2.9	3.7	3.4	3.8	5.3
FSJ	N	3	1	5	13	18	16	409	494	26	28
	Mean	149.9	177.8	170.2	195.1	209.4	222.9	193.2	213.2	204.0	221.0
	SD	21.4	—	44.6	36.9	38.2	24.6	36.3	31.1	35.4	41.6
FSA	N	3	1	5	13	18	16	409	494	26	28
	Mean	827.1	824.2	886.1	956.9	1026.8	1070.0	955.7	1012.3	1000.5	1064.5
	SD	42.5	—	132.1	124.2	113.6	103.4	104.1	101.3	108.5	156.6
FMS	N	5	3	8	18	19	21	442	520	32	29
	Mean	1.05	1.18	1.00	1.10	1.06	1.05	1.07	1.12	1.05	1.08
	SD	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
FMR	N	4	1	7	18	19	19	420	505	29	29
	Mean	58.5	57.3	58.3	57.6	59.7	60.3	60.1	60.5	61.7	61.5
	SD	4.5	—	4.2	3.6	3.4	3.4	3.5	3.3	3.6	4.4
FMJ	N	4	1	7	18	19	19	420	505	29	29
	Mean	117.3	134.3	123.5	144.0	126.7	162.2	141.8	168.3	162.1	177.3
	SD	28.5	—	34.3	27.3	30.3	28.9	30.6	26.1	31.8	30.2
FMA	N	4	1	7	18	19	19	420	505	29	29
	Mean	792.3	824.2	799.5	840.0	825.3	912.9	848.8	922.9	917.9	965.9
	SD	106.5	—	110.0	102.0	90.5	115.6	94.4	95.9	101.6	120/9

<sup>a</sup>See Tables 1-3 for abbreviations.

females based on subsistence strategy in eight variables (Table 6.). Equestrian hunter-gatherers have longer humeri with significantly larger head diameters compared to VHH, WIH, and BHG. They also generally have the largest and most robust femora. Late Woodland (WIH) females are more robust at the subtrochanteric region of the femur

compared to other females, but VHH females have a significantly greater FMJ than WIH females. Unlike the males, females do not particularly cluster in the multivariate analyses by subsistence similarities (Figure 2). Humeral head diameter and HMA separate females on CAN 1 (correlation = 0.34,  $p < 0.0001$ ), while HMS and HMR

**Table 5. Comparison of males by subsistence strategy.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c</sup>
HML	1.83	0.1209	WHG <sup>A</sup> >WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup>
<b>HHD</b>	4.35	0.0018	EHG <sup>A</sup> >WHG <sup>AB</sup> >VHH <sup>AB</sup> >WIH <sup>B</sup> >BHG <sup>B</sup>
HMS	2.54	0.0388	BHG <sup>A</sup> >WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
HMR	1.69	0.1505	WHG <sup>A</sup> >WIH <sup>A</sup> >EHG <sup>A</sup> >BHG <sup>A</sup> >VHH <sup>A</sup>
<b>HMA</b>	2.97	0.0193	EHG <sup>A</sup> >WHG <sup>AB</sup> >BHG <sup>AB</sup> >VHH <sup>B</sup> >WIH <sup>AB</sup>
FML	1.84	0.1197	EHG <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup>
FHD	1.43	0.2216	EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup> >WIH <sup>A</sup>
FSS	3.36	0.0098	WIH <sup>A</sup> >BHG <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup>
FSR	2.61	0.0350	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
FSJ	2.18	0.0703	WIH <sup>A</sup> >VHH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
FSA	3.51	0.0076	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
<b>FMS</b>	3.43	0.0088	BHG <sup>AB</sup> >VHH <sup>A</sup> >WHG <sup>AB</sup> >EHG <sup>AB</sup> >WIH <sup>B</sup>
FMR	3.96	0.0035	EHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
FMJ	5.23	0.0004	EHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
FMA	4.97	0.0006	EHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>

<sup>a</sup>Bolded variables show significant ( $p \leq 0.05$ ) differences based on both ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

**Table 6. Comparison of females by subsistence strategy.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c</sup>
HML	4.39	0.0017	EHG <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup> >VHH <sup>A</sup>
<b>HHD</b>	10.62	<0.0001	EHG <sup>A</sup> >WHG <sup>AB</sup> >VHH <sup>C</sup> >WIH <sup>C</sup> >BHG <sup>C</sup>
HMS	1.52	0.1876	BHG <sup>A</sup> >WIH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup>
HMR	1.36	0.2463	EHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup> >WHG <sup>A</sup>
HMA	1.80	0.1282	EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup> >WIH <sup>A</sup> >BHG <sup>A</sup>
<b>FML</b>	8.31	<0.0001	EHG <sup>A</sup> >WHG <sup>AB</sup> >WIH <sup>AB</sup> >BHG <sup>AB</sup> >VHH <sup>B</sup>
<b>FHD</b>	5.50	0.0002	EHG <sup>A</sup> >VHH <sup>B</sup> >WHG <sup>AB</sup> >BHG <sup>AB</sup> >WIH <sup>B</sup>
FSS	1.37	0.2415	EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >BHG <sup>A</sup>
<b>FSR</b>	4.42	0.0016	WIH <sup>A</sup> >EHG <sup>AB</sup> >VHH <sup>B</sup> >WHG <sup>B</sup> >BHG <sup>B</sup>
<b>FSJ</b>	2.98	0.0189	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>AB</sup> >WHG <sup>AB</sup> >BHG <sup>B</sup>
<b>FSA</b>	4.80	0.0008	WIH <sup>A</sup> >EHG <sup>AB</sup> >VHH <sup>ABC</sup> >WHG <sup>BC</sup> >BHG <sup>C</sup>
FMS	1.13	0.3403	VHH <sup>A</sup> >WIH <sup>A</sup> >EHG <sup>A</sup> >BHG <sup>A</sup> >WHG <sup>A</sup>
FMR	2.24	0.0637	EHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >BHG <sup>A</sup> >WHG <sup>A</sup>
<b>FMJ</b>	5.56	0.0002	VHH <sup>A</sup> >EHG <sup>AB</sup> >BHG <sup>AB</sup> >WIH <sup>B</sup> >WHG <sup>AB</sup>
<b>FMA</b>	4.89	0.0007	EHG <sup>A</sup> >VHH <sup>AB</sup> >WIH <sup>AB</sup> >WHG <sup>B</sup> >BHG <sup>B</sup>

<sup>a</sup>Bolded variables show significant ( $p \leq 0.05$ ) differences based on both ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

have the highest coefficients on CAN 2 (correlation = 0.17,  $p = 0.0635$ ). For the femur, FMA and FMJ are primarily responsible for the distinctions between females (CAN 1: correlation = 0.31,

$p < 0.0001$ )—separating the EHG from other groups. Subtrochanteric size and strength play a role in separating the WIH from other groups on CAN 2 (correlation = 0.18,  $p = 0.1683$ ).

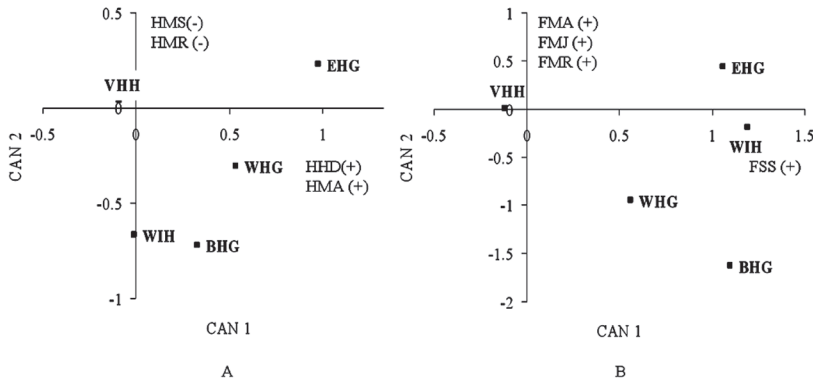


Figure 1. Plot of first two canonical correlations for male humeri (A) and femora (B) showing separation of groups by subsistence strategy. See text for correlations and significance of each canonical axis. Variables on each axis are the canonical coefficients with the greatest weight. The plus and minus signs indicate the direction.

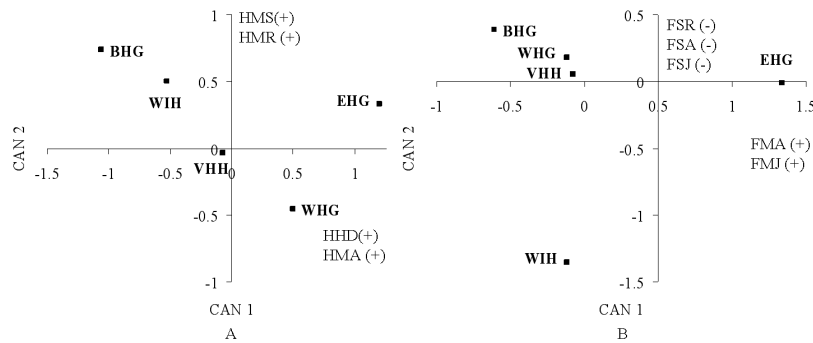


Figure 2. Plot of first two canonical correlations for female humeri (A) and femora (B) showing separation of groups by subsistence strategy. See text for correlations and significance of each canonical axis. Variables on each axis are the canonical coefficients with the greatest weight. The plus and minus signs indicate the direction.

**Sexual Dimorphism**

There are some clear temporal patterns in long bone sexual dimorphism (Table 7). Humeral robusticity (HMR) and area (HMA), for example, are greater in BHG and WHG males but shift to being greater in females among the later WIH, VHH, and EHG. Sexual dimorphism in the femur remains generally constant in length and head diameter, but decreases through time in FSS, FSJ, and FMS and mostly increases through time in FMJ and FMA.

Analysis of variance results indicate that the interaction of sex and subsistence strategy was significant for most of the variables analyzed, which shows that the pattern or amount of sexual

dimorphism differs based on subsistence pattern (Table 7). As a result, sexual dimorphism was also examined separately for each subsistence group. Broad-spectrum hunter-gatherers exhibit significant sexual dimorphism in size (HML, HHD, FML and FHD) only. None of the structural shape or robusticity measures exhibit significant sexual dimorphism, but femur subtrochanteric (FSS) and midshaft (FMS) shape are nearly significant ( $p = 0.0944$  and  $0.1028$ , respectively). However, the sample size is relatively small for BHG, so the results must be viewed with extreme caution. Similar results were found for WHG, with the addition of males having a significantly greater femoral midshaft AP/ML ratio. It is the VHH that exhibit the greatest number

of variables that show statistically significant sexual dimorphism, but this could be an artifact of the much larger sample used for VHH. There is significant sexual dimorphism in all the humeral variables, with males generally having larger but relatively weaker humeri. As expected, VHH males have relatively larger (FML, FHD, FSA, and FMA), stronger (FSJ and FMJ) more AP elongated femora (FSS and FMS) than females.

**Geographical Location**

**Same-Sex Comparisons**

Table 8 presents the summary statistics for each variable by sex and geographical location. Males from the southern Plains have smaller head

diameters for both bones and a greater AP/ML ratio at the midshaft of the femur compared to northern and central Plains males (Table 9). Northern Plains males have significantly more gracile humeri and more platymeric (AP flattened) femur subtrochanteric diaphyses than central or southern Plains males (Table 9). Figure 3 shows the multivariate canonical plots for male humeri (A) and femora (B). For both bones, CAN 1 (humerus: correlation = 0.34,  $p < 0.0001$ ; femur: correlation = 0.39,  $p < 0.0001$ ) separates the northern Plains from the central and southern Plains. Humeral midshaft robusticity (HMR), HMA, and FSS are the primary variables separating the northern Plains males from males in the other geographical regions. The southern Plains males are distinct from northern and central Plains males on CAN 2 (humerus: correlation = 0.20,  $p = 0.0002$ ; femur: correlation = 0.24,  $p < 0.0001$ ) because they have more robust humeri and less circular femoral midshafts.

Females exhibit a very similar pattern of variation to that of the males, with southern Plains females having smaller long bone head diameters (HHD, FHD) and a greater midshaft AP/ML ratio (FMS) compared to the other two geographical regions (Table 10). Likewise, northern Plains females have more gracile humeri (HMR) and a more platymeric femoral diaphysis (FSS). The primary difference between males and females is that southern Plains females differ significantly from northern and central Plains females in all femur midshaft variables. This geographic patterning is also discernable among the females in both the humerus (Figure 4A) and femur (Figure 4B) based on the multivariate analyses. The first canonical axes (humerus: correlation = 0.19,  $p = 0.0082$ ; femur: correlation = 0.43,  $p < 0.0001$ ) primarily separate the southern Plains females from the central and northern Plains females based on humeral robusticity and head diameter and femoral shape and midshaft robusticity, while CAN 2 (humerus: correlation = 0.11,  $p = 0.1692$ ; femur: correlation = 0.20,  $p = 0.0086$ ) segregates the central Plains females that have larger humeri and more circular femoral diaphyses. However, the second canonical correlation for the humerus is not significant and therefore no firm conclusions can be drawn.

### Sexual Dimorphism

A few of the variables (HMR, HMA, and FMR) show a possible, but not significant, geographical patterning for sexual dimorphism. However, ANOVA results demonstrate a significant interaction between the effects of sex and geographical area for 11 of the 15 variables (Table 11). Therefore, sexual dimorphism was analyzed within geographical areas. Significant sexual dimorphism is observed in all size variables of the humerus and femur, but only in some of the shape and strength variables (Table 11). Northern Plains groups exhibit the greatest number of variables with significant sexual dimorphism. Interestingly, FMS is significantly sexually dimorphic in the northern and central Plains but not in the southern Plains.

### SUBSISTENCE STRATEGY IN THE NORTHERN PLAINS

Regional comparison of subsistence groups was only possible for the northern Plains due to sample size. In the multiple comparison tests there

**Table 7. Sexual dimorphism by subsistence strategy.**

Variable <sup>3,4</sup>	% Sexual Dimorphism <sup>1,2</sup>				
	BHG	WHG	WIH	VHH	EHG
HML <sup>5</sup>	<b>6.4</b>	<b>8.5</b>	<b>8.0</b>	<b>7.2</b>	<b>4.5</b>
HHD	<b>15.6</b>	<b>9.9</b>	<b>13.7</b>	<b>12.7</b>	<b>11.1</b>
HMS <sup>5</sup>	-2.7	-2.9	-1.4	<b>-2.2</b>	-2.1
HMR	2.0	2.1	-2.1	<b>-4.4</b>	<b>-4.7</b>
HMA <sup>5</sup>	8.8	1.7	-1.0	<b>-5.6</b>	3.0
FML <sup>5</sup>	<b>6.9</b>	<b>6.3</b>	<b>7.3</b>	<b>8.2</b>	<b>5.3</b>
FHD <sup>5</sup>	<b>13.9</b>	<b>11.6</b>	<b>13.4</b>	<b>11.3</b>	<b>9.6</b>
FSS <sup>5</sup>	18.1	6.7	<b>10.7</b>	<b>2.6</b>	4.8
FSR <sup>5</sup>	3.2	1.2	-2.1	-0.6	0.0
FSJ <sup>5</sup>	18.7	14.7	6.5	<b>10.3</b>	8.3
FSA <sup>5</sup>	15.0	9.0	4.2	<b>5.9</b>	6.4
FMS <sup>5</sup>	12.4	<b>9.4</b>	-0.3	<b>5.66</b>	2.8
FMR <sup>5</sup>	-2.1	-1.2	1.0	0.7	-0.3
FMJ <sup>5</sup>	14.5	17.1	<b>28.0</b>	<b>18.3</b>	9.4
FMA <sup>5</sup>	4.0	4.9	<b>10.6</b>	<b>8.7</b>	5.2

<sup>1</sup>% Sexual Dimorphism = male mean – female mean / female mean \* 100.

<sup>2</sup>Bolded variables are statistically significant at  $p \leq 0.05$ .

<sup>3</sup> See Tables 1-3 for abbreviations.

<sup>4</sup>See Table 4 for sample sizes.

<sup>5</sup>Significant ( $p \leq 0.05$ ) sex and subsistence interaction

**Table 8. Summary Statistics by Geographical Location and Sex.**

Variable <sup>a</sup>	Statistic	NP		CP		SP	
		F	M	F	M	F	M
HML	N	333	371	85	103	48	47
	Mean	300.3	321.7	300.6	320.3	296.8	321.5
	SD	14.6	14.4	13.0	18.6	15.0	13.7
HHD	N	334	375	80	103	48	51
	Mean	41.2	46.4	41.2	46.5	39.9	45.0
	SD	2.3	2.4	2.4	2.6	2.3	2.1
HMS	N	339	381	110	125	62	70
	Mean	1.40	1.37	1.39	1.38	1.41	1.36
	SD	0.1	0.1	0.1	0.2	0.2	0.1
HMR	N	334	371	79	102	47	50
	Mean	42.4	40.3	43.4	42.4	44.2	43.4
	SD	3.1	3.1	3.1	3.5	3.7	2.7
HMA	N	333	370	84	102	46	47
	Mean	896.6	831.6	928.4	959.5	942.9	912.6
	SD	151.5	141.0	167.9	275.7	220.1	174.9
FML	N	384	447	97	117	47	53
	Mean	417.0	450.2	416.8	449.4	417.4	449.8
	SD	21.3	19.6	18.9	20.6	18.2	17.7
FHD	N	377	444	77	103	46	50
	Mean	42.5	47.2	42.2	47.4	41.4	46.0
	SD	2.1	2.2	2.4	2.5	2.3	1.7
FSS	N	369	428	97	116	39	42
	Mean	0.74	0.76	0.79	0.85	0.80	0.83
	SD	0.1	0.1	0.1	0.1	0.1	0.1
FSR	N	362	425	77	102	38	41
	Mean	63.6	63.3	64.2	64.0	64.8	63.8
	SD	3.7	3.3	3.9	4.3	3.0	3.2
FSJ	N	356	419	75	100	30	33
	Mean	194.5	213.8	193.2	214.9	187.2	203.5
	SD	36.6	29.6	39.1	41.0	31.5	25.9
FSA	N	356	419	75	100	30	33
	Mean	955.8	1011.7	969.5	1033.2	905.7	1008.1
	SD	107.7	100.1	110.5	133.1	79.2	87.2
FMS	N	384	447	97	116	47	52
	Mean	1.05	1.11	1.07	1.11	1.14	1.18
	SD	0.1	0.1	0.1	0.1	0.1	0.1
FMR	N	377	444	77	102	46	49
	Mean	59.8	60.4	60.2	60.7	62.1	61.0
	SD	3.5	3.4	3.8	3.8	3.0	2.9
FMJ	N	356	435	75	100	35	37
	Mean	140.7	167.2	141.8	171.2	155.7	164.1
	SD	31.2	26.2	31.2	30.8	30.1	22.0
FMA	N	356	435	75	100	35	37
	Mean	845.0	919.7	854.0	933.4	905.8	916.4
	SD	96.5	97.8	96.5	113.8	81.8	75.5

<sup>a</sup>See Tables 1-3 for abbreviations.

**Table 9. Comparison of Males by Geographical Location.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c</sup>
HML	0.36	0.6987	NP <sup>A</sup> >SP <sup>A</sup> >CP <sup>A</sup>
<b>HHD</b>	7.90	0.0004	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>B</sup>
HMS	0.23	0.7956	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>
<b>HMR</b>	33.72	<0.0001	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>B</sup>
HMA	22.47	<0.0001	CP <sup>A</sup> >SP <sup>A</sup> >NP <sup>B</sup>
FML	0.08	0.9186	NP <sup>A</sup> >SP <sup>A</sup> >CP <sup>A</sup>
<b>FHD</b>	7.42	0.0007	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>B</sup>
<b>FSS</b>	55.75	<0.0001	CP <sup>A</sup> >SP <sup>A</sup> >NP <sup>B</sup>
FSR	1.65	0.1937	CP <sup>A</sup> >SP <sup>A</sup> >NP <sup>A</sup>
FSJ	1.76	0.1732	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>
FSA	1.74	0.1771	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>
<b>FMS</b>	11.81	<0.0001	SP <sup>A</sup> >NP <sup>B</sup> >CP <sup>B</sup>
<b>FMR</b>	1.05	0.3502	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>A</sup>
<b>FMJ</b>	1.26	0.2856	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>
<b>FMA</b>	0.83	0.4361	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>

<sup>a</sup>Bolded variables show significant ( $p \leq 0.05$ ) differences based on both ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

**Table 10. Comparison of Females by Geographical Location.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c</sup>
HML	0.21	0.8087	CP <sup>A</sup> >NP <sup>A</sup> >SP <sup>A</sup>
<b>HHD</b>	4.82	0.0085	NP <sup>A</sup> >CP <sup>A</sup> >SP <sup>B</sup>
HMS	0.90	0.4061	SP <sup>A</sup> >NP <sup>A</sup> >CP <sup>A</sup>
<b>HMR</b>	7.61	0.0006	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>B</sup>
HMA	1.70	0.1834	CP <sup>A</sup> >SP <sup>A</sup> >NP <sup>A</sup>
FML	0.24	0.7878	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>A</sup>
<b>FHD</b>	6.81	0.0012	NP <sup>A</sup> >CP <sup>AB</sup> >SP <sup>B</sup>
<b>FSS</b>	24.74	<0.0001	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>B</sup>
FSR	2.77	0.0635	SP <sup>A</sup> >CP <sup>A</sup> >NP <sup>B</sup>
FSJ	0.30	0.7374	NP <sup>A</sup> >CP <sup>A</sup> >SP <sup>A</sup>
FSA	0.95	0.3880	SP <sup>A</sup> >NP <sup>A</sup> >CP <sup>A</sup>
<b>FMS</b>	20.22	<0.0001	SP <sup>A</sup> >CP <sup>B</sup> >NP <sup>B</sup>
<b>FMR</b>	10.19	<0.0001	SP <sup>A</sup> >CP <sup>B</sup> >NP <sup>B</sup>
<b>FMJ</b>	3.72	0.0248	SP <sup>A</sup> >CP <sup>B</sup> >NP <sup>B</sup>
<b>FMA</b>	6.51	0.0016	SP <sup>A</sup> >CP <sup>B</sup> >NP <sup>B</sup>

<sup>a</sup>Bolded variables show significant ( $p \leq 0.05$ ) differences based on both ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

are no significant same-sex differences between subsistence groups in the northern Plains for humeral structural properties (Tables 12 and 13). Furthermore, there is no temporal pattern of variation. Equestrian (EHG) males have significantly

larger humeral heads than horticulturalist (VHH and WIH) males (Table 12), and equestrian females have larger and longer humeri compared to females from the other subsistence groups (Table 13). There are also no significant differences based on subsistence strategy in femoral properties among males (Table 12). There are significant differences in femur torsional strength and area among females from the northern Plains with EHG having significantly stronger bones than WIH or WHG.

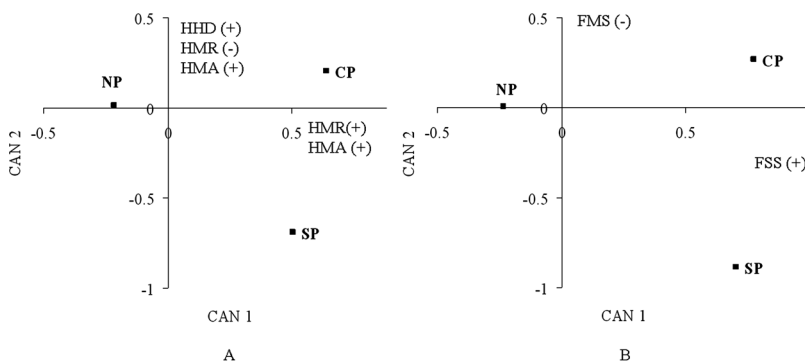


Figure 3. Plot of first two canonical correlations for male humeri (A) and femora (B) showing separation of groups by geographical location. See text for correlations and significance of each canonical axis. Variables on each axis are the canonical coefficients with the greatest weight. The plus and minus signs indicate the direction.

## DISCUSSION

### Subsistence Strategy

Numerous studies of Native American skeletons have demon-

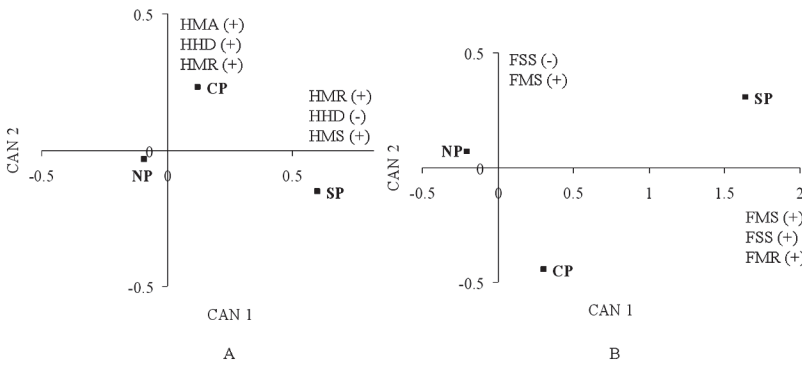


Figure 4. Plot of first two canonical correlations for female humeri (A) and femora (B) showing separation of groups by geographical location. See text for correlations and significance of each canonical axis. Variables on each axis are the canonical coefficients with the greatest weight. The plus and minus signs indicate the direction.

regional variation, in general, these studies have shown that hunter-gatherer males have more robust long bones and a greater femoral midshaft AP/ML ratio than horticultural males. In addition, hunter-gatherers have a greater level of sexual dimorphism than horticulturalists in long bone robusticity and femur midshaft shape (Larsen 1997; Ruff 1987, 2000a). Many re-

**Table 11. Sexual Dimorphism by Geographical Area.**

Variable <sup>c,d</sup>	% Sexual Dimorphism		
	NP	CP	SP <sup>ab</sup>
HML	<b>7.1</b>	<b>6.5</b>	<b>8.3</b>
HHD	<b>12.6</b>	<b>12.9</b>	<b>12.6</b>
HMS	<b>-2.0</b>	-0.9	<b>-3.5</b>
HMR <sup>e</sup>	<b>-4.7</b>	-2.1	-1.8
HMA <sup>e</sup>	<b>-7.2</b>	3.3	-3.2
FML	<b>8.0</b>	<b>7.8</b>	<b>7.8</b>
FHD <sup>e</sup>	<b>11.0</b>	<b>12.3</b>	<b>11.1</b>
FSS <sup>e</sup>	<b>1.9</b>	<b>7.9</b>	3.6
FSR <sup>e</sup>	-0.5	0.0	-1.5
FSJ <sup>e</sup>	<b>10.3</b>	<b>11.2</b>	7.4
FSA <sup>e</sup>	<b>5.9</b>	<b>6.6</b>	3.2
FMS <sup>e</sup>	<b>5.5</b>	<b>3.4</b>	4.4
FMR <sup>e</sup>	<b>1.7</b>	0.8	-1.6
FMJ <sup>e</sup>	<b>18.4</b>	<b>20.4</b>	5.12
FMA <sup>e</sup>	<b>8.9</b>	<b>9.3</b>	1.1

<sup>a</sup>% Sexual Dimorphism = male mean – female mean / female mean

<sup>b</sup>Bolded variables are statistically significant at  $p \leq 0.05$ .

<sup>c</sup>See Tables 1-3 for abbreviations.

<sup>d</sup>See Table 8 for sample sizes.

<sup>e</sup>Significant ( $p \leq 0.05$ ) sex and geographical location interaction.

strated significant variation in long bone structural properties between hunter-gatherers and horticulturalists (e.g., Bridges 1989, 1991; Larsen 1981; Ruff 1987, 1994; Ruff and Larsen 1990; Ruff et al. 1984). While there appears to be some

researchers have argued that the observed differences between subsistence groups, especially in femur morphology, are due to the high mobility required by hunter-gatherer males to acquire game animals compared to the relatively low levels of mobility necessary in subsistence tasks performed by hunter-gatherer females and horticulturalists of both sexes. As Larsen (1995:203) has pointed out, “Ethnographic documentation of mobility patterns in hunter-gatherers indicates that long-distance movement and acquisition of protein resources through hunting is nearly always done by males, whereas in agricultural and industrial societies, like females, males are involved in sedentary tasks.” Similarly, Ruff (1987) argued that as farming becomes more important in societies, males do less hunting and participate more in tasks such as field preparation, crop planting, and pottery making—all of which require relatively less mobility.

While mobility is a possible explanation for the variation seen between hunter-gatherers and horticulturalists in many regions of the United States (e.g., Southwest, Georgia coast, and West Coast), it does not explain the long bone variation seen on the Great Plains. Long bone size and shape are relatively homogeneous among Plains groups from the Archaic to historic period. This is especially true in the regional analysis of northern Plains subsistence groups. Furthermore, in the canonical plots (Figures 1 and 2), there are nearly identical patterns of group separation whether

**Table 12. Comparison of Males from the Northern Plains by Subsistence Strategy.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c</sup>
HML	3.18	0.0139	EHG <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup>
<b>HHD</b> <sup>d</sup>	4.67	0.0032	EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>AB</sup> >WIH <sup>B</sup>
HMS	1.27	0.2812	WIH <sup>A</sup> >VHH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
HMR <sup>d</sup>	4.15	0.0066	EHG <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup>
HMA	2.64	0.0334	WHG <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup> >BHG <sup>A</sup>
FML	1.58	0.1782	EHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup> >BHG <sup>A</sup>
FHD <sup>d</sup>	1.26	0.2881	EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >WIH <sup>A</sup>
FSS	3.59	0.0069	EHG <sup>A</sup> >WIH <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup> >BHG <sup>A</sup>
FSR <sup>d</sup>	3.36	0.0188	WIH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup>
FSJ <sup>d</sup>	2.12	0.0968	WIH <sup>A</sup> >WHG <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup>
FSA <sup>d</sup>	5.22	0.0015	WIH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >VHH <sup>A</sup>
FMS	4.37	0.0018	BHG <sup>A</sup> >VHH <sup>A</sup> >EHG <sup>A</sup> >WHG <sup>A</sup> >WIH <sup>A</sup>
FMR	1.72	0.1616	EHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
FMJ <sup>d</sup>	1.97	0.1173	EHG <sup>A</sup> >WIH <sup>AB</sup> >VHH <sup>AB</sup> >WHG <sup>B</sup>
FMA <sup>d</sup>	2.26	0.0805	EHG <sup>A</sup> >WIH <sup>AB</sup> >VHH <sup>AB</sup> >WHG <sup>B</sup>

<sup>a</sup>Bolded variables show significant ( $p \leq 0.05$ ) differences based on ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

<sup>d</sup>There are no BHG males from the northern Plains with this variable.

**Table 13. Comparison of Females from the Northern Plains by Subsistence Strategy.**

Variable <sup>a,b</sup>	F	p-value	Paired Group Differences <sup>c,d</sup>
<b>HML</b>	7.11	0.0001	EHG <sup>A</sup> >WIH <sup>A,B</sup> >WHG <sup>A,B</sup> >VHH <sup>B</sup>
<b>HHD</b>	8.71	<0.0001	EHG <sup>A</sup> >WHG <sup>A,B</sup> >VHH <sup>B,C</sup> >WIH <sup>C</sup>
HMS	0.83	0.4793	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
HMR	2.95	0.0329	EHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
HMA	1.36	0.2537	EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup> >WIH <sup>A</sup>
<b>FML</b>	12.39	<0.0001	EHG <sup>A</sup> >WIH <sup>A,B</sup> >WHG <sup>B</sup> >VHH <sup>B</sup>
<b>FHD</b>	8.31	<0.0001	EHG <sup>A</sup> >VHH <sup>B</sup> >WHG <sup>B</sup> >WIH <sup>B</sup>
FSS	5.25	0.0015	EHG <sup>A</sup> >WHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup>
FSR	6.50	0.0003	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
<b>FSJ</b>	3.06	0.0283	WIH <sup>A</sup> >EHG <sup>AB</sup> >VHH <sup>AB</sup> >WHG <sup>B</sup>
<b>FSA</b>	6.29	0.0004	WIH <sup>A</sup> >EHG <sup>A</sup> >VHH <sup>AB</sup> >WHG <sup>B</sup>
FMS	1.73	0.1605	VHH <sup>A</sup> >EHG <sup>A</sup> >PWIH <sup>A</sup> >WHG <sup>B</sup>
FMR	2.32	0.0748	EHG <sup>A</sup> >WIH <sup>A</sup> >VHH <sup>A</sup> >WHG <sup>A</sup>
<b>FMJ</b>	5.35	0.0013	EHG <sup>A</sup> >VHH <sup>AB</sup> >WIH <sup>B</sup> >WHG <sup>B</sup>
<b>FMA</b>	5.20	0.0016	EHG <sup>A</sup> >VHH <sup>AB</sup> >WIH <sup>B</sup> >WHG <sup>B</sup>

<sup>a</sup>Bolded variables show significant differences based on both ANOVA and multiple comparisons results.

<sup>b</sup>See Tables 1-3 for abbreviations.

<sup>c</sup>Groups ordered sequentially from largest to smallest mean. Groups with same superscript letter do not differ significantly based on multiple comparisons.

<sup>d</sup>There are no BHG females from the northern Plains in the study sample.

humeral or femoral properties are used. It is unlikely that humeral variables are affected by mobility, although a systemic effect is possible (Lieberman 1996). Most likely, the level of mobility did not change dramatically on the Plains through time. Moreover, there probably was not the marked sex difference in mobility among Plains groups that occurred in other geographical regions. Even among semisedentary horticulturalists on the Plains, nearly the entire village (both males and females) traveled long distances on bison hunts, and as Wood (1998:7) has highlighted, "when villagers were on their annual bison-hunting expeditions away from their lodges, their life scarcely differed from that of their nomadic neighbors." How far back in time this hunting practice began is unknown, but it is likely very ancient (Blakeslee 1994; Wood 1998). Regardless, except maybe for a decrease in the absolute percent sexual dimorphism in FMS, the results of this study suggest that if femur shape and robusticity reflect mobility (but see Lieberman et al. 2004 and Wescott 2006a for criticism of this idea), then Plains horticulturalists were as mobile as earlier hunter-gatherers.

Cole (1994) has suggested that Plains horticulturalists might have been more mobile than earlier Woodland hunter-gatherers because Plains Woodland groups have relatively circular femoral midshafts compared to Plains villagers. However, while VHH were found to have a greater femoral midshaft AP/ML ratio than WHG in this study, VHH have a slightly more circular femur midshaft shape compared to BHG. Furthermore, the difference between VHH and the two hunter-gatherer groups in FMS is not significant, but the lack of significance between VHH and BHG could be due to the very small BHG sample size (5 males and 3 females). Overall, the results of this study suggest that VHH were just as mobile, but not more so, than earlier hunter-gatherers. The emphasis on bison as a protein source throughout most of the Plains occupation resulted in both hunter-gatherers and horticulturalists (of both sexes) traveling long distances several times a year.

Contrary to other geographical regions, the transition from hunting-gathering to horticulture on the Plains did not result in a temporal decline

in long bone strength. This is not surprising as Lehmer and Wood (1977) have argued that VHH were probably more similar to the mixed horticultural and pastoral societies of the Old World than they were to other Native American horticulturalists. This suggests that VHH should be morphologically more similar to hunter-gatherers than horticultural groups in other regions, which is, in fact, what is seen. Ruff (1994:244), for example, compared femoral cross-sectional properties of Plains Villagers to hunter-gatherers from the Georgia coast and concluded that "Plains Villagers had a relatively rigorous lifeway, similar in terms of overall activity level to hunter-gatherers from the Georgia coast."

Interestingly, while there are few same-sex univariate differences between subsistence groups, multivariate analyses do suggest that Plains males cluster partially by subsistence similarities based on humeral and femoral morphology (Figure 1). This suggests that subsistence activities performed by males may have changed enough through time to cause some alterations in long bone morphology. However, much of the variation in males may also be associated with temporal increases in size and robusticity. Through time, humerus midshaft robusticity decreases while femur midshaft size (FMA) and robusticity (FMR and FMJ) increases (see Figure 1B: CAN 2). This pattern is seen in both EHG and VHH, suggesting that they have changed in a similar manner.

The horse revolutionized life in the Great Plains, and frequent horseback riding has been found to cause a higher prevalence of lower limb arthritis and heel bone fractures (Reinhard et al. 1994) as well as elongation in the acetabulum (Erickson et al. 2000) of Plains Indians. Biomechanically, frequent horseback riding should cause greater ML loadings on the femur midshaft, resulting in a more circular cross section (Ruff 1994). However, the introduction of the horse does not appear to dramatically affect long bone structural morphology on the Plains. Ruff (1994) found no significant changes in Arikara femur midshaft strength or shape with the introduction of the horse, and the results from this study show that there are few significant differences between EHG and other hunter-gatherers. Furthermore, it

is unclear if the differences that do occur were triggered by activity, diet, genetics, or some other factor. Plains equestrian nomad males (but not females) have relatively (although not significantly) circular femoral midshafts and slightly greater midshaft area and torsional strength compared to the other Plains hunter-gatherers and VHH, which would be expected since EHG males frequently traveled on horseback. The relatively greater femur length and head diameter of EHG, however, could be the result of dietary differences. There is evidence that historic equestrian groups had better access to protein sources than other Plains groups (Prince 1998), which would result in greater stature and body size. Finally, the EHG sample used in the study were primarily Siouan speakers and the majority of VHH were Caddoan speakers (Wescott 2001). This suggests a possible genetic difference between the historic EHG and VHH.

For females, the multivariate plots do not show any clear subsistence based separation of groups for either the humerus or femur. Ruff (1987, 2000a) has argued that females do not differ greatly in femoral structural properties because females in both horticultural and hunter-gatherer societies perform relatively sedentary tasks. Therefore, it is not surprising that females do not pattern by subsistence practice based on femur morphology. It is, however, surprising that females do not cluster based on subsistence similarities for the humerus. Bridges and colleagues (Bridges 1989, 1991; Bridges et al. 2000) have found that humeral strength increased and humeral asymmetry decreased among females with the transition from hunting and gathering to horticulture in the Southeast. Therefore, one would expect WIH and VHH females to cluster based on humeral morphology, but this is not the case in the Plains. However, the most significant change among females observed by Bridges and colleagues was in humeral asymmetry, with horticulturalists having greater symmetry. Unfortunately, symmetry was not evaluated in this study, but see Wescott and Cunningham (2006) for a discussion of temporal changes in symmetry among the Arikara.

Like same-sex comparisons, sexual dimorphism in the Plains is difficult to interpret in part because of the small sample size for BHG and

WHG. Ruff (1987, 2000a) has argued that hunter-gatherers are generally more sexually dimorphic than horticulturalists because of a greater sexual division of labor in hunter-gather societies. Sexual dimorphism in several of the structural variables, including FMS, is greater among early hunter-gatherers compared to later horticulturalists. This is consistent with Ruff's (1994) argument that sexual dimorphism in mobility was declining through time, and consistent with overall subsistence-related trends. However, in the Plains there are fewer significant differences between BHG or WHG in humeral or femoral structural properties compared to VHH. Most of the significant differences (HML, HHD, FML, FHD) among Plains hunter-gatherers are strictly related to body size. The greater number of variables exhibiting statistically significant sexual dimorphism among later VHH could be the result of sample size bias and therefore should be viewed with caution. The pattern, however, may also be consistent with the idea that sexual division of labor is an important factor. In the Plains, sexual division of labor may have increased with the transition from hunting-gathering to horticulture. Hunting strategies in the Plains probably changed little through time (Wood 1998), with both males and females traveling on the hunt (Blakeslee 1994). Conversely, among most Plains horticulturalists, females did all the work required to prepare fields, plant, harvest, and process the crops (Parks 2001). Wescott and Cunningham (2006) found that humeral and femoral strength increased through time among Arikara females as they intensified crop production, but males changed little in femoral strength during this period. However, it should be noted that Wescott and Cunningham (2006) also observed that sexual dimorphism declined from the Extended to the Postcontact Coalescent periods and then increased again in the Disorganized Coalescent. They argued that this pattern of sexual dimorphism may reflect dietary stress more than differences in sexual division of labor. Furthermore, Ruff (1994) found that late Woodland and Middle Missouri samples exhibited about the same level of sexual dimorphism in FMS as hunter-gatherers from other geographical regions. Coalescent populations, however, fell within the range of sexual dimorphism of agriculturalists from other

regions. While the pattern of sexual dimorphism observed in this study may be due to sample size bias and have little biological or behavioral significance, when combined with the results from Wescott and Cunningham (2006) and Ruff (1994), the results of this study suggest that sexual dimorphism, at least on the Great Plains, may reflect some presently unknown factor or set of factors other than sexual division of labor.

### Geographical Location

The most common explanations for variation in long bone size and shape between populations based on geographical location are differences in genes, terrain, and climate (Lovejoy et al. 2002, 2003; Ohman and Lovejoy 2001; Pearson 2000; Ruff 1999, 2000a; Stock 2006). Overall, the pattern of geographical variation in long bone morphology among Plains Native Americans does not appear to reflect differences in terrain relief, but climatic factors may be responsible for some of the variation observed.

### Terrain Relief

Ruff (1999, 2000a) has argued that terrain relief may be the most influential factor in femur torsional strength between groups, with populations from rugged, mountainous terrains having stronger femora than populations from areas with relatively lower relief, such as the Georgia coast. In general, terrain relief does not vary greatly from north to south in the Plains. However, the northern Plains has more rugged areas and deeper river trenches than the central or southern Plains. This would suggest that if terrain is playing a role in the differences seen in populations from different geographical regions of the Plains, northern Plains populations should have more robust femora. Northern Plains males, however, do not differ significantly from central or southern Plains males for FSR, FSJ, FMR, or FMJ. Northern Plains females do have greater FSJ values than central or southern Plains females, although the difference is not significant. But, for FSR, FMR, and FMJ, northern Plains females have smaller values than central or southern Plains females. Overall, the pattern of geographical variation in morphology among Plains Native Americans does

not appear to be caused by terrain relief.

### Climate

Climate has been shown to correlate with long bone morphology. Pearson (2000), for example, discovered that the long bones from populations in cold environments are generally more robust than those from populations in warm climates. Similarly, Stock (2006) observed that robusticity among hunter-gatherers correlated negatively with mean temperature, and Weaver (2003) found that cold-adapted populations have larger mean femoral heads relative to length and thick, circular femoral midshafts. Warm-adapted populations, on the other hand, have smaller femoral heads relative to length and less circular midshafts.

The most marked differences between geographical groups on the Plains are that northern populations have relatively small and gracile humeral diaphyses (HMA and HMR, respectively), and relatively small (FSA) but platymeric (small FSS value) femur subtrochanteric regions. Southern Plains populations, on the other hand, have humeri with small heads but robust diaphyses and femora with small heads but robust and AP elongated (high AP/ML ratio) midshaft cross sections. These patterns generally hold true for both males and females, and may be related to climatically-induced variation in adult physique and growth and development patterns. As would be predicted based on average temperature differences (higher in south than north), southern Plains groups have relatively smaller humeral and femoral head diameters relative to bone length than northern Plains groups. Furthermore, midshaft femoral diaphyses from the northern Plains are generally circular while those in the southern Plains are AP elongated. The significantly larger FMS of southern Plains males is due to a smaller ML diameter (MLS is significantly smaller in southern Plains males) compared to the males in the other two geographical regions, and not to a larger AP diameter (APS). Southern Plains males do not differ from central or northern Plains males in FML, but they do have significantly smaller FHD. Femur head diameter is highly correlated with body build (Auerbach and Ruff 2004), which suggests that southern Plains males were leaner relative to stat-

ure than their northern and central Plains counterparts – an observation that would be expected based on climatic differences. Additionally, Wescott (2006b), using data on American Black and White subadults, showed that most of the variation in APS during growth is related to growth in femur length. The midshaft ML diameter, on the other hand, is primarily correlated with growth in FHD. Since southern Plains males have smaller femur head diameters, it would be expected that they also have significantly smaller midshaft ML diameters than the other groups. Furthermore, since femur length does not differ significantly between groups, neither should APS. These two patterns are exactly what were observed in this study. The means for APS are 30.0, 30.1, and 30.5 for northern, central, and southern Plains males, respectively, and the means for MLS are 27.0, 27.4, and 25.7, respectively. There are no significant differences between groups in APS. However, the southern Plains males are significantly smaller in their ML diameter. This same argument also explains the differences between females based on geography.

The differences in FSS and humeral morphology are a little more difficult to explain, but are probably also tied to climate related differences in body build. Femur subtrochanteric shape is established early in life as subadults learn to walk with an adult gait pattern (Wescott 2006c). Wescott (2006c) found that differences between populations in FSS are probably associated with differences in hip breadth relative to stature. This idea is also supported by Ruff (2000b) who found that femur subtrochanteric strength scales positively with the product of body mass and mediolateral body breadth (hip breadth). Body breadth data are not available for the Plains groups used in this study, but it is reasonable to assume that northern Plains groups had slightly wider hips than those from the southern Plains (Ruff 1995; Weaver 2003). If so, this would explain the greater platymeria (ML expansion at subtrochanteric) among northern Plains Indians. Hip breadth correlates positively with latitude, and femur subtrochanteric ML bending loads increase with increasing hip breadth (Ruff 1995). The north-south dichotomy in humeral head diameter and diaphyseal

robusticity is also likely to be associated with differences in physique. Although the humerus is not a weight bearing bone, Ruff (2000b) found that strength of the upper limb bones scaled similarly to those of the lower limb.

While climatic differences appear to explain some of the variation seen on the Plains, it may not explain differences in diaphyseal robusticity. In the Plains, robusticity of the humerus and femur does not appear to correspond to variation in temperature. Robusticity has been found to have a negative correlation with temperature (Pearson 2000; Stock 2006), suggesting that populations from the northern Plains should be slightly more robust than those from the southern Plains. However, for both sexes, HMR and FMR are greatest in the southern Plains and least in the northern Plains, with the northern Plains being significantly different from the central and southern Plains. Femur midshaft area and FMJ are also significantly greater among southern Plains females compared to their NP and CP counterparts. Therefore, when body size is controlled for, northern Plains Indians are slightly less robust than central or southern Plains groups. This would suggest that climatic factors are not the primary influences on the geographical patterning seen in long bone robusticity, and that activity patterns or other factors may have a greater impact on diaphyseal robusticity among Plains Native Americans.

Of course, Ruff (1994) noticed this north-south dichotomy in FMS and suggested that it provided evidence that southern Plains groups were more mobile than those in the northern Plains. However, while there were most likely differences in hunting and horticultural practices in both time and space due to cultural and environmental factors, there is no clear archaeological evidence that the farming activities of southern Plains horticulturalists differed greatly from northern Plains horticulturalists or that southern Plains hunter-gatherers differed greatly from northern Plains hunter-gatherers in their overall subsistence activities. Blakeslee (1994) argues that bison were more common in the northern than central or southern Plains during the Woodland period. This might suggest that southern Plains groups had to travel greater distances to acquire bison, at least

during the Woodland period. However, there are no significant differences in FMS in males or females between central and northern Plains populations. Mobility would also not explain the differences in humeral morphology, nor would it explain why the difference between northern and southern Plains FMS is due to a reduced ML breadth in southern Plains groups. Higher mobility should cause greater AP loading on the femur and therefore result in a greater AP diameter in the southern Plains, but this is not the case. Therefore, it is unlikely that differences between the northern and southern Plains in femoral morphology are related to levels of mobility.

#### Sexual Dimorphism

There are no clear geographical patterns in the level of sexual dimorphism on the Plains. For all of the size and structural variables examined, there is little difference in the degree of sexual dimorphism between northern, central, and southern Plains populations. However, there are a greater number of significant differences between males and females in the northern Plains compared to the other geographical regions. The reason for this remains unclear, but is probably related to the larger number of individuals from VHH sites in the northern Plains sample.

One of the more interesting patterns of sexual dimorphism observed in this study is that, at least in multivariate space, males tend to cluster based partially on subsistence similarities, while females cluster based on geographical location. This same pattern has also been demonstrated in other studies. Larsen (1997) showed that femoral midshaft torsional strength (J) closely parallels subsistence strategy in males from the Stillwater Marsh in Utah, the Georgia coast, and Pecos Pueblo in New Mexico, but in females, torsional strength is more clearly aligned with geographical location. He argued that the geographical patterning in females was associated with the ruggedness of the terrain. However, while Wescott (2001) also found geographical patterning among females from the Great Basin, Great Plains, Texas Gulf Coast, Southwest, and northeastern Prairies, he found no support for the hypothesis that terrain relief was the primary causal factor. The results from this study also suggest that terrain relief is not a primary causal fac-

tor. The geographical patterning of females probably reflects migration and mating patterns as well as climatic-induced differences in body build. For males, however, activity levels associated with subsistence practice may be great enough to alter long bone morphology beyond that caused by genetic and environmental factors. However, there is also a strong temporal component to male morphology, regardless of subsistence.

#### GENERAL CONSIDERATIONS

The lack of statistical significance between subsistence and geographical groups in this study may be in part due to the methods used and the source of the data. External measurements can be used to estimate cross-sectional properties, but this can result in greater overlap between groups than may be found using cross-sectional data (see discussion in Wescott 2006a). Furthermore, it is not possible to directly compare external and cross-sectional results, but external dimension data do appear to provide the same general pattern of variation as cross-sectional data. Ruff (1987) found the same pattern of long bone adaptation due to subsistence strategy when comparing external dimensions and cross-sectional values of hunter-gatherers, agriculturalists, and industrialists. Furthermore, Larsen's (1981) study of hunter-gatherers and horticulturalists from Georgia was later supported by cross-sectional data on the same sample by Ruff et al. (1984), and Cole (1994) and Ruff (1994) found similar patterns among northern Plains groups using external dimensions and cross-sectional properties, respectively. In addition to using estimated cross-sectional properties, the data for this study comes from a database with measurements from multiple scientists. As a result, some noise is produced by interobserver error that could increase the amount of variation observed. However, previous research with this data suggests that interobserver error is minimal (Wescott 2005).

Finally, one thing that is clear from the low canonical correlations for both males and females is that there is greater variation within subsistence groups than between subsistence groups. This is also true for geographical variation. Some of the within subsistence group variation is undoubtedly due to the wide geographical distribution and tem-

poral span within the subsistence groups. However, great variation within subsistence groups was also found when comparing groups from the northern Plains only. This suggests that there is considerable individual variation in long bone morphology within subsistence groups, and probably reflects individual differences in body build and how subsistence related activities were carried out.

### CONCLUSIONS

In general, long bone morphology in the Great Plains is relatively homogeneous through time and space. As pointed out by Cole (1994), stresses associated with the transition from hunting-gathering to horticulture on the Plains were not sufficient to cause the immense morphological changes seen among Native Americans in some geographical regions of the United States. Native American adaptations to the Plains environment were unique compared to other regions, and the dichotomy between hunter-gatherers and horticulturalists has probably been overemphasized. As Wood (1998:7) has argued, "despite the many contrasts between the two groups, however, the mode of life of the horticulturalists was not as profoundly different from that of the nomads as has been claimed." The importance of bison to Plains Native Americans throughout time and space resulted in cultural and biological continuity.

Despite the relatively homogeneous nature of long bones from the Plains, two intriguing dichotomies were observed. One is that northern Plains Indians generally have humeri with large heads but gracile shafts, and femora with large heads that are more platymeric (ML expanded) at subtrochanteric and more circular at midshaft compared to southern Plains groups. Most likely, this pattern of variation is associated with climatic differences and not levels of mobility or terrain relief. The second dichotomy is that the pattern of variation parallels subsistence strategy for males and geographical location for females. Perhaps most of the variation in the Plains is due to climatic factors but the subsistence activities of males may result in sufficient mechanical loads and be specific enough to cause subsistence specific patterns of morphology.

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