Early Holocene Morphological Variation in Hunter-Gatherer Hands and Feet

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Abstract
The Windover mortuary pond dates to the Early Archaic period (6,800-5,200 years ago) and constitutes one of the earliest archaeological sites with intact and well-preserved human remains in North America. Unlike many prehistoric egalitarian hunter-gatherers, the Windover people did not practice a sex-based division of labor, rather they shared the load. We explore how mobility and subsistence, as reconstructed from archaeological data, influenced the morphology of hand and foot bones of this population. Using length-width ratios to account for trait size and taking the natural log of the ratio to account for sexual dimorphism, we analyzed 10 variables (4 carpal and 6 tarsal. We identified differences in the rear-and midfoot regions that suggest the Windover occupation was engaging in heavy impact mobility. In particular, females exhibit greater variation and higher mean averages than males for size of shock-absorbing bones. We identified sex-based differences in carpal bones, with females exhibiting greater variation and higher mean ratios in most variables compared to males. Despite widespread behavioural evidence on contemporary populations for human lateralization for hands and feet, we found no evidence of either handedness or footedness in Windover. The lack evidence for footedness was expected due its minimal impact on walking gait but the lack of evidence for handedness is surprising given that modern ethnographic studies have shown strong handedness in hunter-gatherers during tool and goods manufacture. If the archaeological evidence for a shared division of labor is true, we have potentially uncovered evidence for a heavier activity load in females.

1.INTRODUCTION

A sex-based division of labor is seen across most human societies for the majority of evolutionary history and contributes to size-based morphological variation between the sexes [1] [2]. The wealth of ethnographic data on extant hunter-gatherers provides insights into activities ascribed to each of the sexes. Applying what we know about extant hunter-gatherer behavior to the bioarchaeological record, we can link muscular-skeletal markers to habitual activities. Physical markers of activity include geometric variation in bone structure and function due to biomechanical loading [3], diaphyseal structure [4-8], degenerative joint disease (DJD), osteoarthritis, muscular-skeletal markers (MSM) [9], and dental wear patterns relative to tool manufacture [10, 11].

1.1 Mobility Activity

Hunter-gatherer mobility can be described as residential (moving camp to a new location as in seasonal occupation of resource rich areas) and logistical (individuals and/or smaller groups temporarily split from the main group for shorter foraging trips or longer hunting trips) [12, 13]—this is particularly true for mobile hunter-gatherers that specialize in terrestrial resources [14-16]. There is some evidence for sex-based variation in hunter-gatherer mobility; modern Hadza hunter-gatherer males engage in greater daily walking distances at faster speeds than females [17, 18].

Distal limbs have been implicated to a greater degree than upper limbs in reflecting habitual activity due to the biomechanical forces arising from locomotive substrate (i.e., terrains on which activities are conducted), distances travelled in a day, and relative speed of locomotion [7, 9, 17-30]. Of interest to this study is how biomechanical stress from mobility and footedness might affect the tarsals. The ground reaction force generated by the bare (or minimally shod) foot contacting the ground is transmitted through the subtalar skeleton, with peak forces at heel-strike through the calcaneus and at heel-off through the metatarsophalangeal articulations [31]. Thus, during normal locomotion, the typical bipedal heel strike transmits body mass from the tibia to the rear foot (talus and calcaneus) to the ground [32] while the shock of impact is absorbed by the midfoot (navicular, cuboid, and cuneiform bones) [32]. The calcaneus is most affected by the rear heel strike and calcaneal tuber length (as a proxy for Achilles tendon moment arm length) is correlated with running economy (long calcaneal tuber = greater energy cost) [33] Most data from extent hunter-gatherers [30, 34] and barefoot populations suggest a rear heel strike [35] is preferred among experienced runners. Dorsal spurs on the calcaneus are linked to increased activity while plantar spurs are linked to standing, inactivity, and excess weight [27]. While footedness in humans develops in late childhood (11-12 years old) with a right skew [36, 37], its influence on walking gait is not significant and is unlikely to affect the muscular-skeletal system in the absence of other evidence of lateralization [38]. Thus, regions of the foot may be differential shaped by daily logistical mobility that emphasizes either slow walking and stationary weight-bearing activity (such as might occur when foraging) or rapid locomotion such as brisk walking or running that requires greater shock absorption. And, if subsistence based activities are assigned via sex [2, 6], there may be sex-differences in how these regions of the feet vary.

1.2 Domestic economies

Domestic economies include subsistence and tool manufacture, which supports subsistence activities. Subsistence covaries with biological factors (e.g., habitat, reproduction, health) and cultural factors (e.g., social organization, sedentism, mobility). A comprehensive analysis of 229 hunter-gatherer diets, eco-environmental data, and plant-to-animal dietary ratios found that most populations consume similar amounts of carbohydrates (30-35% of the diet) except in more extreme environments (i.e., increases in desert and tropical grasslands and decreases in higher latitudes) [39]. Indeed, there is a strong clinal pattern of variation in male and female caloric contributions to diet. Subsistence contributions by sex are inversely correlated with effective temperature, a combined measure of the intensity and annual distribution of solar radiation [12, 40]. Higher latitudes and colder climates rely more on male caloric contributions from big game hunting while temperate and tropical regions rely more heavily on female caloric contributions across the spectrum (e.g., small game, fishing, and plants) [39]. In general, males tend to increase foraging activities in more stable productive habitats [41] and females tend to decrease labor in subsistence activities when males are hunting big game (focusing instead on activities like weaving and cordage) [42].

Ethnographic data indicate that domestic economies such as tool making, child care and carrying, butchering/food preparation, textiles, and carrying firewood and water create physical strain [14, 43-45]. Increased reliance on tools is linked to evolutionarily more gracile bodies [46] but tool manufacturing and use are detectable on the body through increased upper limb robusticity [25] and lateralization, or side preference [47]. Unimanual activities (e.g., spear use) leave a distinct mark of directional asymmetrical in the upper limbs compared to bimanual activities such as grinding or rowing [48]. Indeed, extant hunter-gatherers exhibit strong hand preference specifically when making and using tools [49, 50] which suggests mosaic progression to extreme lateralization we see in modern populations [47]. And, there is evidence in the archaeological record of sidedness varying between the sexes [22, 51]. While domestic economies vary across groups, they tend to be sex-based and more frequently involve lateralized repetitive stress compared to subsistence and mobility [48]. Thus, bioarchaeological evidence of subsistence activities and tool manufacture may found in repetitive stress to the musculo-skeletal system and result in lateralized MSM, DJD, and osteoarthritis of the limbs involved. Carrying loads may place additional weight-bearing biomechanical stress on the foot and the domestic economies may serve to differentiate the wrists.

1.3 Aims

The focus of this paper is to explore whether or not logistical mobility and domestic economies (subsistence and tool manufacture) are archaeologically visible in the feet (tarsals) and hands (carpals) and, if so, whether or not they reflect a sex-based division of labor. Much attention has been paid to sexual dimorphism in carpal and tarsal elements in forensic contexts and with applications to sexing skeletons in bioarchaeology; these studies have had varied success with most pointing to the calcaneus and sometimes talus as the most diagnostic elements [52-64]—for a review see [65]. Carpals and tarsals were chosen for this study for two reasons. First, they are heavily implicated in the daily activities of hunter-gatherers (e.g., mobility, use of weapons, tool-making, domestic economies). Second, they are less likely to be influenced by the noise created from conflicting signals of genetics and lifestyle that obfuscates differentiation of ultimate and proximate causes of variation that plagues the long bones [21]. Third, dense and small bones, such as carpals and tarsals, are among the better-preserved elements in the human body (Henderson 1987; Mann 1981; Waldron 1987) and if daily activities are visible in these elements, we are potentially able to capture data that might otherwise be lost in less well-preserved skeletons.

We examined carpal and tarsal data from the Florida Early Archaic Windover Site which contains the remains of a population of hunter-gatherers experiencing a major climate change in North America and, along with it, a change in domestic economies. Warmer climate was driving big game north and broad-spectrum foraging was emerging as the primary subsistence economy, de-emphasizing the dietary contribution of males and increasing the contributions of females. We generated research questions based on general cross-cultural patterns identified in hunter-gatherers (Section 1) and specific patterns identified at the Windover Site (Section 2). As such, research questions are placed at the end of Section 2.

2. MATERIALS (BIOARCHAEOLOGICAL CONTEXT)

The Windover mortuary pond archaeological site (8BR46) is a National Historic Landmark dating to the Early Archaic Period (7500-5000 BCE) with calibrated radio-carbon dates from 9000 to 7929 BP. In general, the North American Archaic Period (8000 to 1000 BC) is characterized by hunting-gathering subsistence economies with dietary staples including nuts, seeds, and shellfish [66]. The Florida Archaic Period follows the same pattern (e.g., broad spectrum hunting, fishing, and plant gathering and use of freshwater resources) with increased exploitation of coastal shellfish and marine resources. The comparatively wetter climate [67] created an abundance of resources and and subsistence strategies were no longer dominated by big game. The broad spectrum foraging strategy that emerged is reflected in more complex tool kits [66, 68].

Windover was used as a mortuary pond with 5-6 short periods of activity, peaking at 7450 BP [68]. Burials furthest from the pond edge at time of excavation dated to the earliest period of mortuary pond use and those closest, more recent. Roughly 100 burials were undisturbed with fully articulated bones; ages ranged from infancy to over sixty-five, with 52% classified as subadults [69]. Most individuals were buried within 24 to 48 hours after death (Doran 1992; Dickel 1988, Hauswirth 1991) in a flexed position, on the left side with heads oriented to the west, and pinned by sharpened stakes approximately 1m below the surface of the peat [70]. The nearly neutral pH of the pond (6.1-6.9) created ideal conditions for preservation of both skeletal and soft tissues; allowing researchers to sequence DNA from preserved brain matter [70], reconstruct diet from preserved stomach contents [71], and study textile industries [72]. The population exhibited predominantly good health and included individuals of extremely advanced age (50+) for hunter-gatherer groups which reflects local resource abundance [73] and medical practices [71, 74-77]. Common to hunter-gatherer populations, adults of both sexes exhibited a high incidence of osteoarthritis [78], frequent enamel defects [79, 80], and skeletal trauma [76]. Overall, female health was worse than males [77, 81]

2.1 Mobility

The bog was strategically located between the Indian River coastal lagoon system and the St. John's River, an area rich in marine, fresh water, and terrestrial resources, which indicates that the population did not have to travel long distances between seasons [74] and did not fission into smaller groups between visits to the pond [77]. Seasonal mobility is indicated by analysis of preserved stomach contents which were from plants and fruits maturing during July and October. In addition, growth ring data recovered from mortuary stakes indicated the wood was harvested in late summer/early fall [82]. Ultimately, however, the residential mobility of the Windover population was limited to a constrained geographic area around the bog with most evidence pointing to emergence of sedentism [77].

2.2 Subsistence economies

Paleodietary analysis from carbon and nitrogen bone-collagen values and archaeobotanical information suggest exploitation of riparian resources rather than the more common Florida Archaic use of marine mammals or terrestrial fauna such as deer or rabbit [71]. Males and females did not have significantly different isotope values for major dietary components [77, 81]. Based on ethnographic data, the resource rich environment fostered by a milder wetter climate suggests greater reliance on female caloric contributions to diet [39]and this is supported by grave goods--both males and females were found with materials for hunting small mammals, reptiles, and fish [75]. There is evidence of some specialization because only male graves atlatl components, spears, lithic projectiles, and hollow point awls (for making fishing nets) and only females and subadult graves contained direct evidence for food processing (e.g., butchered bone, mortar and pestle, containers) [72, 75].

2.3 Tool economies

Analysis of tools found amongst the grave goods suggests tool material choice (not type) was sex-based; females preferred organic materials (e.g., shell, carapace) while males preferred antler bone [74, 75]. Few tool types were exclusive to one sex which suggests few activities were specific to one sex [75]. Females also tended to have more decorative items [75] and were found exclusively with materials for plant-based medicine [71, 74, 75]. Interestingly, stone tools only play a cameo in the story of tools at Windover [74] while female goods (textiles, baskets, containers, medicines) have a starring role across the history of the pond. The absence of internment with stone tools suggests a cultural emphasis on the labor of women and products from both men and women in the domestic economy rather than an emphasis on male big-game hunting [74]. This may be an outcome of climate change [66, 68] rapidly altering domestic roles from the Paleoindian to the Early Archaic periods.

2.4 Activity Reconstruction

DJD at Windover has been analyzed in two separate studies [78, 83] using different methods but both finding high rates of DJD consistent with prehistoric hunter-gatherer lifestyles [78, 83]. DJD frequency in the cervical spine is particularly high in females and may be explained by food or palm leaf (for textile fibers) processing activities [83] or carrying heavy loads [78] both of which are supported by grave good evidence [72, 74, 75]. Males exhibit greater DJD in the lumbar region which they were carrying heavy loads (perhaps game or goods during seasonal camp relocation) or stressed from repetitive motions related to hide processing [83]. Elbows were commonly affected which might be interpreted as male atlatl throwing but females exhibited more DJD in wrist elbows and shoulders than males [83] which suggests a shared activity [78]. Wrists exhibited little evidence of DJD (3/97 left and right wrists affected) but females had more hand trauma [83] and males had a higher frequency of severe DJD in both hands (18% of the sample) [78]. Significant bilateral degeneration of talar-calcaneal articular facets was noted in 37% of individuals [78], which might reflect high mobility [27], possibly running [33, 35, 84, 85]. There were some overall sex-based patterns in DJD with males exhibiting more knee and hip damage on the left and females exhibiting more severe change on the right [78], which might suggest footedness and increased mobility in males with more shock to the feet.

An examination of muscle insertion sites [86] found low levels of habitual stress (indicative of stressful repetitive activity) but muscle insertion sites were fairly robust. As with the DJD results, there is much overlap between the sexes in scores further supporting the notion that most activities were shared. The lack of asymmetry in MSM, particularly in males due to the use of the atlatl, suggests a lack of repetition in this activity or other activities which exert symmetrical force on the upper limbs and obscure the lateralization of spear-throwing—possibly kayaking [86]. Analysis of fractures suggests interpersonal violence (affecting male crania and, less frequently, the post cranial skeleton) but the majority of trauma came from accidents with females slightly more affected than males. Ribs (often on the right side) were the most fractured in both sexes with ulnar fractures in second place. The vertebra exhibit evidence of compression fractures (more frequent in females and equal to ulna fractures in incidence) consistent with falls when landing in an upright position or carrying heavy loads. Overall, fracture patterns suggest accidents related to logistical mobility in the uneven intercoastal terrain and heavy underbrush [76].

2.5 Research Questions

1. Mobility
    a) Are there differences between weight-bearing and shock absorbing tarsals as suggested by previous research indicating heavy load carrying and high mobility or running?
    b) Is there asymmetry in tarsals as suggested by asymmetrical DJD in lower limbs and fracture patterns?
2. Subsistence
    a) Is there a between-sex difference in carpal bones based on previous research showing greater hand trauma and domestic economy production in females?
    b) Is there asymmetry in carpal bones reflecting handedness in complex tasks for making tools and textiles?

3. METHODS

Carpal and tarsal elements with standard anatomical reference points intact were included from adults with well-defined features used in sex assessment (given the focus on sex-based morphological variation) resulting in a sample of 44 (27 males, 17 females), but sample size varies by measurement. All measurements were taken on right and left sides, when available. Length and width were measured on four carpal bones, four tarsal bones, and the weight-bearing areas of the talus (trochlea) and calcaneus (load arm). Raw data were explored for significant outliers using Grubb's statistic.

Table 1: Measurements

Element	Measurement	Orientation	Description
Scaphoid	Length	proximal	scaphoid tubercle-lateral most point
	Width	palmar medial	bisection of scaphoid ridge
Capitate	Length	palmer	proximal-distal end
	Width	lateral	thinnest point
Lunate	Length	proximal	proximal-distal end
	Width	proximal	medial-lateral sides
Hamate	Length	lateral	proximal end-distal ridge (between metacarpal facets)
	Width	lateral	most medial to most lateral side of the facet
Calcaneus	Length	lateral	(Steele and Bramblett 1988)
	Width	superior	(Steele and Bramblett 1988)
	Load arm length	superior	(Steele and Bramblett 1988)
	Load arm width	superior	(Steele and Bramblett 1988)
Talus	Length	superior	(Steele and Bramblett 1988)
	Width	superior	(Steele and Bramblett 1988)
	Trochlea tibia length	superior	(Steele and Bramblett 1988)
	Trochlea tibia width	superior	(Steele and Bramblett 1988)
Navicular	Length	distal	medial tuberosity to lateral cuneiform facet
	Width	inferior	between intermediate and medial cuneiform facets
Int. Cuneiform	Length	superior	proximal and distal midpoint
	Width	superior	thickest middle portion

There are two major methodological concerns for this size-based morphological study: sexual dimorphism [87-89] and trait size variation [90, 91]. The inherent difference between two variables may be confounded by relative difference in size—comparing the intermediate cuneiform to the talus or comparing male to female. A common resolution to sexual dimorphism in size-based studies is to take a ratio of two variables, such as length and width [87-93]. The issue of trait size variation is one common to asymmetry studies [94-96] and often resolved by scaling data to the natural log [92, 95]. The natural log of ratio dataset is symmetric, homoscedastic, and retains the original linear scale of standard deviation to the mean (the spread or variation of the data) [97]. Thus, we have taken the natural log, $\log_n$, of the absolute value of length-to-width ratio, *L:W*, per bony element, *x*:

$$\log_n|x(L:W)|$$

This resulted in a total of four carpal variables (capitate, hamate, lunate, scaphoid) and six tarsal variables (calcaneus, calcaneus load arm, intermediate cuneiform, navicular, talus, talus, trochlea tibia). These data are included as Supplementary Tables 1 and 2.

Log transformed ratio data were tested for the normal distribution. A two-way (sex by class) univariate General Liner Model (GLM) assessed differences between tarsal classes (weight bearing, shock absorbing). A multivariate GLM assessed differences in carpal bones. A two-way (sides by individual) univariate GLM was used to assess the presence of directional asymmetry in both tarsal and carpal bones [94-96]. All results were evaluated relative to confidence intervals, power, and estimated effect size.

4. RESULTS

Outliers identified by Grubb's statistic were inspected and removed if determined to be data entry error. Extreme values not identified as outliers were retained. Data were transformed to mitigate the confounding effect of trait size and sexual dimorphism as previously described. All variables were normally distributed (Supplementary Table 3). Descriptive data for all variables by sex are found in Supplementary Table 4.

Are there differences between weight-bearing and shock absorbing tarsals as suggested by previous research indicating heavy load carrying and high mobility or running? Exploratory analysis suggested that females have larger shock-absorbing bones than males and shock-absorbing bones were larger than weight-bearing bones (Figure 1, left). The two-way univariate GLM (Levene=001, p=1.00) indicated no significant between-sex difference or interaction between sex and bone class but the statistical significance for differences between shock-absorbing and weight-bearing tarsals is high (Table 2, Figure 1, right).

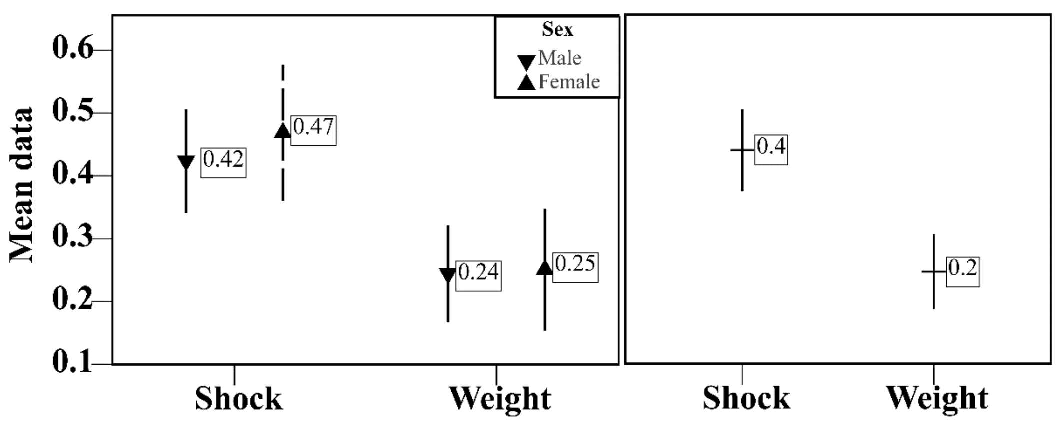

Figure 1: Confidence intervals for weight-bearing and shock absorbing mean pooled sex (left) and by sex (right)

Table 2: Univariate GLM Analysis of Tarsal Scaled Ratio Data

										95% CI	
Test	**F**	**df**	**Sig**	**ηp**	**Power**		**Mean**	**SE**	**n**	**Lower**	**Upper**
Sex(S)	1.83	1	0.41	0.65	0.09	M	0.33	0.03	237	0.27	0.39
						F	0.36	0.04	142	0.28	0.44
Class(C)	108.06	1	0.06	0.99	0.59	S	0.45	0.04	129	0.37	0.53
						W	0.25	0.03	250	0.19	0.31
S*C	0.14	1	0.71	0.00	0.07	S-M	0.42	0.05	82	0.33	0.52
						W-M	0.24	0.04	155	0.17	0.52
						S-F	0.47	0.07	47	0.34	0.60
						W-F	0.25	0.05	95	0.16	0.34

Is there asymmetry in tarsals as suggested by asymmetrical DJD in lower limbs and fracture patterns? The two-way univariate GLM did not indicate any lateralization of the foot bones, or 'footedness' and no further testing was indicated (Supplementary Table 5).

Is there a between-sex difference in carpal bones based on previous research showing greater hand trauma and domestic economy production in females? Exploratory plots (Figure 2) show that females have larger carpal ratios than males except for the hamate. Results of a multivariate GLM suggest potentially significant differences between the sexes (Pillai's Trace F=2.811, p=0.059, ηp=0.0.398). The univariate individual tests generated by the multivariate GLM (Table 3) suggest the lunate and scaphoid contribute most to the potentially significant differences. The visualization of 95% confidence intervals (Figure 3) indicates that females have greater ranges that encompass most male values.

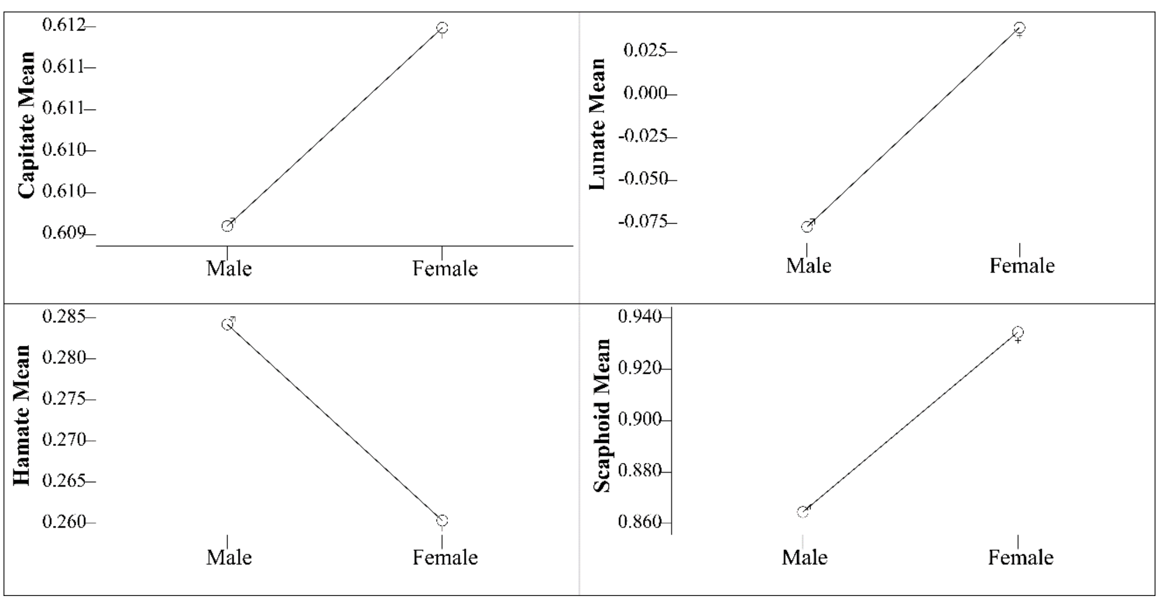

Figure 2: Means plots for carpals

Table 3: Multivariate GLM Analysis of Carpal Ratio Scaled Data

											95% CI	
	Levene	**Sig**	**F**	**df**	**Sig**	**ηp**	**Power**	**Mean**	**SE**	**n**	**Lower**	**Upper**

A	3.22	0.09	2.85	1	0.11	0.13	0.36	M	0.60	0.02	28	0.56	0.63
								F	0.65	0.02	21	0.60	0.70
B	2.15	0.16	1.11	1	0.31	0.05	0.17	M	0.28	0.02	21	0.24	0.32
								F	0.25	0.02	14	0.20	0.30
C	4.32	0.05	2.71	1	0.12	0.12	0.35	M	-0.08	0.03	27	-0.15	-0.01
								F	0.01	0.04	20	-0.08	0.10
D	0.22	0.64	1.10	1	0.31	0.05	0.17	M	0.85	0.03	22	0.79	0.92
								F	0.91	0.04	19	0.82	1.00

[1]A-Capitate; B-Hamate; C-Lunate; D-Scaphoid

[2]M, male; F, female

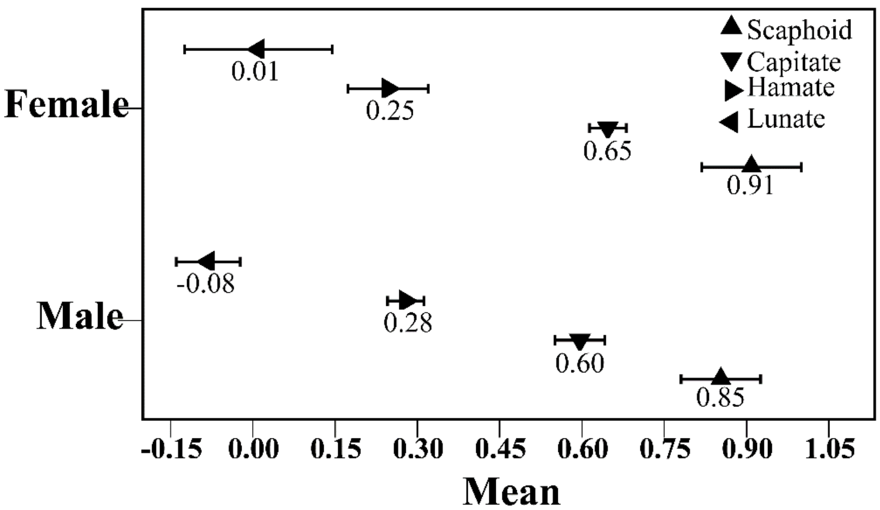

Figure 3: Carpal ratio scaled data 95% confidence intervals by sex

Is there asymmetry in carpal bones reflecting handedness in complex tasks for making tools and textiles? The two-way univariate GLM did not indicate any lateralization of the hand bones, or 'handedness' and no further testing was indicated (Supplementary Table 5).

5. DISCUSSION

Archaeological data reconstructing the environment surrounding the mortuary pond suggest that the larger region of the Windover population was rich with riparian and terrestrial resources due to climate warming at the start of the Early Archaic. As megafauna distributions increased in latitude, Windover subsistence strategies increasingly relied less on big-game hunting more on broad spectrum foraging [67, 82]. Grave good analysis and activity reconstructions suggest heavy overlap between the sexes in domestic economies rather than a strict sex-based division of labor [75-78, 86].

5.1 Tarsal Variation

Based on previous analysis, we speculated whether load carrying might influence differences between weight-bearing and shock absorbing tarsals. A univariate two ways (sex by class) GLM indicated no significant between-sex differences or significant interaction between sex and class (shock-absorbing, weight-bearing). The power for both these tests is extremely low and confidence interval data suggests there may be a statistically undetected significant between-sex difference. This potential difference is not consistent with sexual dimorphism because shock-absorbing bone summary data suggest higher female mean ratios and a greater range than males while the weight-bearing bone summary data suggest no differences (same mean, females contained within the male interval). This female specific pattern is reflected in the results of the pooled sex test for difference between weight-bearing and shock absorbing bones. Reaching the threshold for statistical significance was likely prevented by the observed power (59%) which likely was not high enough to capture the difference. Thus we feel confident in interpreting these results as biological significant. Females have larger mean ratios for shock-absorbing bones than males. We expected the reverse in both sexes—greater stress on weight-bearing tarsals (talus and trochlea, calcaneus and load arm) due to heavy load-carrying, as evidenced by the increased bilateral degeneration of the talar-calcaneal articular surfaces [78], cervical DJD in females [78], and presence of lumbar DJD in males [78]. The rate of fractures attributed to accidents suggested high mobility in a rough terrain (which certainly describes intercoastal regions) and our results may reflect this as well.

Clinical evidence of the effect on the foot due to barefoot walking and running during growth and development suggests it lengthens the foot at the expense of width and flattens the arches [35, 84, 85]—this is true even when controlling for potentially confounding effects of demographic variation [84]. The navicular is a key stone bone in the arches of the foot that is impinged during foot strike by the talus and other cuneiforms. Structurally linking the rear- and mid-foot, it bears the transmission force of weight during the push-off phase of locomotion and experiences highly localized stress in middle one-third of the bone, which makes it prone to fracture in highly athletic individuals [98-101]. Anatomically, the intermediate cuneiform articulates with the navicular proximally and second metatarsal distally. The second metatarsal-intermediate cuneiform joint is a highly stable key stone joint with limited mobility. Injury to the joint occurs via direct force from load applied to the base of the foot or indirect forces from a longitudinal force applied to a plantarflexed foot [102, 103]:1826, which is particularly pronounced in barefoot populations [30, 35, 84, 85, 104]. Bone alterations resulting from these biomechanical stresses might be the source of the higher length to width ratios in shock-absorbing tarsals observed in this study. We posit that females may have navigated a wider range of terrains than males (given their preference for shell tools), might have foraged at greater distances for raw materials (for tools, plant-based medicines, or textiles), or engaged in faster walking and running speeds to cover greater distances. Future avenues of research might be to examine the tubers and spurs on the calcaneus to identify possible differences in locomotion versus weight-bearing activities [27, 33].

5.2 Foot Lateralization

Despite evidence suggesting footedness would not be visible [38, there was bioarchaeological evidence suggesting lateralization in the lower limbs that may have affected the tarsals. In particular, males had greater DJD on the left with knees and hips implicated while females had greater DJD on the right {Smith, 2008 #5573]. These lateral patterns did not translate to differences in the tarsals bones but possible other areas to consider in future studies would be the hallux due to its involvement in the extreme plantarflexion associated with barefoot locomotion [85].

5.3 Carpal Variation

We postulated there might be between-sex differences in carpal bones due to increased hand trauma in females [83] and cervical vertebra DJD possibly linked to food and textile processing activities [72, 74, 83] compared to increased DJD in males [78]. We found evidence to support activity-based variation between the sexes—females had higher mean ratios and greater variation than males. These differences cannot be explained by biology and sexual dimorphism because an analysis of modern humans suggests, that despite anatomical differences in wrist function and rotation, between-sex variation in carpal bones is attributable entirely to relative size which can be accounted for through scaling procedures [105], as we have done. The larger size in females is further evidence that this defies the pattern expected due to male-female size differences. In all but the capitate, the range of female values contains all male values and female ratio means exceed males in all but the hamate.

Does the extreme variation in female carpal bone sizes may reflect inter-individual differences in activity intensity or workloads compared to males? This interpretation is challenging to other studies that have argued for a shared activity load. As reviewed previously, cultures in which male contributions to diet dominate tend to emphasize female labor in domains other than diet (e.g., weaving, cordage) [42]. Perhaps females were previously engaged in many non-subsistence domestic tasks during the Paleoindian period, which was characterized by big game hunting [66]. Then, the climate change in the Early Archaic undermined male contributions to diet as megafauna migrated north [67, 82] and female activities (including a return to intense foraging) dominated.

The absence of stone tools as grave goods is highly uncharacteristic in societies that value male hunting contributions and the emphasis at Windover on artifacts typically associated with female labor (e.g., medicine preparation, containers for carrying goods, decorative items, textiles) lend support to this [74]. Males were associated with tools that suggest their involvement in this domestic labor and activity reconstructions suggest a heavy overlap between the sexes in labor [75-78, 86] but there is also evidence for sex-based division of labor (males and big game hunting, females and plant-based medicine). Indeed, the Windover population is characterized by obvious skeletal markers for health care (e.g., post-fracture bone alignment, surviving childhood stressors) [77, 81, 83] and this care was likely provided by females. Further, the sex-based preference for tool materials suggests a gendered ideology surrounding tasks [75]. While we cannot infer too deeply from the site because it is a mortuary pond and only reflects internment ritual, we can argue that our findings muddy the water a little in terms of the shared load model and point to some increased burden of activity on females, some specialization within females to specific tasks, or some female specific activities.

5.4 Hand Lateralization

Our final area of inquiry was lateralization in the carpal bones due to previous research suggesting that hunter-gatherers exhibited strong handedness when engaged in complex tasks [47, 49, 50]. The complex tool kit at Windover would have provided an avenue for handedness to be archaeological visible but, neither male nor female carpal bones exhibited significant directional asymmetry. We might have expected some lateralization in males due to spear-throwing but the DJD and MSM patterns were shared between the sexes which suggests that males may not have been regularly engaged in spear-throwing, or perhaps the markers of spear-throwing were offset by changes in other aspects of wrist anatomy [106]:238. A previous study on a population with clear handedness identified only two bones exhibiting directional asymmetry, the lunate and trapezium [107] which suggests handedness is not likely to be archaeologically visible.

6. CONCLUSION

Windover females exhibit greater variation (Supplementary Table 4) in seven out of 10 ratio variables and larger means in eight out of ten variables. Clearly, this is not expected were sexual dimorphism were to have influenced the results despite our data transformations to mitigate this effect. Thus, we argue that the observed patterns (in both descriptive data and statistical tests) indicate marking of the female body by activity more so than marking of the male body. A previous study found that Windover females experienced worse health than males [77, 81] and this might be related to their heavier burden of labor. Even if grave goods suggests a shared load, a few sex-based patterns exist with males still associated with big game hunting and females associated with medicine. Further, the raw material for tools is partitioned by sex and would differentiate mobility patterns associated with acquiring tool materials. In addition, females are found exclusively with containers and may have dominated container production (including acquisition of raw materials) or used containers to transport resources to the habitation site—yet to be identified in the archaeological record.

While we might have expected some hand [49, 50] and possibly some foot lateralization [36, 37], we did not find it even if DJD and MSM patterns suggesting there might be some. The lack evidence for footedness was expected due its minimal impact on walking gait [38]. The lack of evidence for handedness is unexpected since modern ethnographic studies on hunter-gatherers have shown strong handedness during tool and goods manufacture [49, 50]. But, handedness in these populations overall have been found to be much less pronounced when compared to modern industrial societies [49]. Although some archaeologists are concerned by the 'tyranny of ethnography' (Wobst 1978), we believe predictions about behavior are an essential part of investigating archaeological populations. Certainly, as demonstrated in this paper, some aspects of behavior are more archaeologically visible than others.

Overall, we can conclude that lateralization in the wrist and foot is not archaeologically visible in this population. Further, we conclude that previous assessments of the high value placed on female labor at Windover [74] is embodied and potentially reflects an asymmetric workload or retention of some sex-based activities. Ultimately, the Windover females tell a much more interesting bioarchaeological story than the males.

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