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. We explore how mobility and subsistence, as reconstructed from archaeological data, influenced the morphology of hand and foot bones of this population. The climate change to warmer weather in the Early Archaic was paralleled by a shift from big game hunting to broad spectrum foraging, however, based on grave goods, Windover people likely maintained sexual division of foraging labor. Grave goods indicate females preferred shells as a raw tool material and were likely exclusively employed in plant-based medicines. Males preferred stone as a raw tool material and were likely exclusively in spear and arrow hunting activities. Males exhibited more evidence of interpersonal trauma. We found evidence of sexual dimorhism in both carpal and tarsal bones, but the results for the tarsal bones are not as statistically robust as those for the carpal bones. Weight-bearing bones were more dimorphic than non-weight bearing bones. Among the all bones investigated, the lunate was by far the most sexually dimorphic. Surprisingly, despite a wealth of ethnographic data on the universality of human handedness, there was no evidence for significant directional asymmetry in the sample. We discuss the implications of these results with regard to the archaeological invisibility of particular behavioral patterns.

Human sex dimorphism is less extreme than most extant and fossil primates (Frayer & Wolpoff 1985; Plavcan 2001). The topic of sex dimorphism is quite broad but can be split into two primary areas: ultimate and proximate, with ultimate causes focused on genetic or epigenetic changes and proximate causes focused on environmentally determined factors that affect individual morphology during the lifespan (Pearson 2000). Ultimate causes include sexual selection (Marlowe & Berbesque 2012) and Life History trade-offs (Stieglitz et al. 2015). In contrast, proximate causes are usually linked to economic activities (e.g., subsistence, occupation) (Holden & Mace 1999).

Egalitarian hunter-gatherer societies are characterized by a sex-based division of labor and clear morphological divisions between the sexes; this pattern is seen across most human societies for the majority of our evolutionary history (Frayer & Wolpoff 1985). A marked reduction in sex dimorphism started roughly 10,000 years ago with changes to male morphology. This resulted from a minimization of the sex-based division of labor due to increased sedentism, decreased big-game hunting, and the advent of plant and animal domestication (Frayer 1980). Using research on extant or ethnographically described egalitarian hunter-gatherer activity patterns and morphology, we can infer past population activity patterns based on skeletal morphology. One challenge for inferring behavior based on ethnographically described hunter-gatherers has been the extreme variation that exists in hunter-gatherer lifeways, even when the focus is solely on one variable (for example, mobility or subsistence). However, the wealth of ethnographic data available do help provide insights into categories of activities and how they impact on muscular-skeletal morphology. Research on this topic ultimately contributes to a better understanding of the cultural parameters of human behavior as shaped by the environment of evolutionary adaptedness (Irons 1998).

Habitual activities physically mark the body via increased biomechanical loading on bones—increased robusticity signals persistent habitual activity. Differences in daily activities include subsistence-related labor, mobility, and other activities. There are several approaches to interpreting behavior from the skeleton, the most robust of which is geometric properties of bone structure and function taken together (Ruff et al. 2006). Another approach to setting expectations for sex dimorphism is data from osteoarthritis studies which can help reconstruct patterns of heavy use-wear. Other studies have found differential patterns of muscular-skeletal markers (Eshed et al. 2004). And, of course, behavioral use of the limbs can have a strong effect on diaphyseal structure (Bridges 1989; Bridges 1995; Ruff 1987b; Ruff 1987c; Schaffler et al. 1985)—the distal limb is more strongly implicated in behavioral differences than the upper limbs (Stock 2006).

Increased variation between males and females for specific parts of the body might suggest different activity patterns, or a sex-based division of labor. The focus of this paper is to explore hunter-gatherer sex dimorphism in ankle and wrist elements (tarsals and carpals) during the Florida Early Archaic Period (6,800-5200 years ago) in a population of hunter-gatherers from the Windover Site. Much attention has been paid to these elements in a forensic context (with applications to sexing skeletons in bioarchaeology) with varied success (Bostanci 1962; Bunning 1964; Gualdi-Russo 2007;

Harris & Case 2012; Hoover 1997; Introna et al. 1997; Kidd & Oxnard 2002; Mastrangelo et al. 2011a; Mastrangelo et al. 2011b; Riepert et al. 1996; Steele 1970; Steele 1976; Steele & McKern 1969)—for a review see (Davies et al. 2014). Here, we focus specifically on how variation in daily activity might increase variation between males and females and induce lateralization of skeletal elements. The wrist and ankles 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 (Pearson 2000). 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).

**Factors Affecting Sex dimorphism**

**Mobility.** Hunter-gatherer mobility falls into two main categories: residential mobility wherein all individuals move camp together to a new location (such as for seasonal occupation of resource rich areas) and logistical mobility wherein individuals or smaller groups splinter from the main residential location (such as for shorter foraging trips or for longer hunting trips) (Binford 1980). There is an incredibly wide range of variation in mobility data for modern hunter-gatherer populations (Kelly 1983) and this includes both number of moves and distance of moves. Greater mobility in hunter-gatherers result in narrower medio-lateral tibial and femoral shafts (relative to anteroposterior shaft) and thicker diaphyseal cortical bone (Pearson 2000). The locomotive substrate is a determinant of foot strike preferences during running, which then influence the biomechanical forces operating on the bones. As a result, lower limb skeletal morphology has been shown to reflect habitual activity patterns (Bridges 1991; Bridges 1995; Carlson et al. 2007; Eshed et al. 2004; Lieverse et al. 2007; Malina & Little 2008; Pearson 2000; Ruff 1987a; Ruff 2000; Shaw & Stock 2009; Stock 2006; Venkataraman et al. 2013; Weiss 2012). For example, the robusticity of the mid-shaft of the femur is particularly implicated in male terrestrial mobility (Stock 2006). 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 (Berbesque et al. 2016; Raichlen et al. 2017) and there is extreme variation in mobility in Australian hunter-gatherer populations too (Carlson et al. 2007). The Hadza study did not examine skeletal elements but the Australian did and found no evidence of sex dimorphism in the lower limb, even in groups with sex-based mobility patterns.

**Subsistence.** Activity patterns for most animals are primarily determined by subsistence activities—how an organism procures its food. Much attention has been paid to subsistence variation in anthropology because it is often a covariate with both biological (e.g., habitat, reproduction, health) and cultural factors (e.g., social organization, sedentism, mobility). Ethnographic data have indicated that (Sahlins 1968) most mobile hunter-gatherers that use terrestrial resources fission and fuse in order to forage on a daily basis (Marlowe 2005; Panter-Brick 2002). A comprehensive analysis of 229 hunter-gatherer diets that considered both eco-environmental data and plant-to-animal dietary ratios found that most populations consumed 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) (Hiatt 1978). 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 (Bailey 1960; Binford 1980)—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 (Hiatt 1978). Female contributions to diet are generally broad and include hunting of small game, fishing, and plant gathering. Females even engage in big game hunting via contributing their knowledge of the environment to males (Biesele & Barclay 2001) or via direct action (Brightman 1996). While males often are the primary big game hunters (particularly in high latitudes), males also gather, fish, and hunt small game (Marlowe 2007). Seasonality also contributes to increased sex-based division of labor; males tend to increase foraging activities in more stable productive habitats (Marlowe 2007). Increases in male big game meat contributions to diet are linked to decreases in female caloric contributions to diet and increases in female labor in other domains (e.g., weaving, cordage) (Waguespack 2005). These sex-based divisions of labor leave their mark on the body and the sexes (Frayer 1980; Ruff 1987b).

**Persistence running.** Walking barefoot, a common practice in many modern traditional societies, diffuses the forces of locomotion across the plantar foot differently than when wearing shoes. The ground reaction force that occurs when the foot is in contact with 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 (Trinkaus & Shang 2008). The use of foot wear reduced peak forces starting after 26,500 BP (Trinkaus & Shang 2008) based on archaeological evidence and resulted in relatively gracile phalanges, narrower hallux space, and narrower pedal breadth (Trinkaus & Shang 2008). Some have argued that barefoot endurance running is useful in traversing the distances involved in tracking herds and big game, but this has been critiqued (Steudel-Numbers & Wall-Scheffler 2009). A running gait typically involves a fore foot strike which decreases effect body mass force during impact by incorporating the ankle via plantarflexion (Hatala et al. 2013; Lieberman et al. 2010), data from the Daasanach of northern Kenya suggest a preference for a rear foot strike during endurance running. As running speed increases, the mid and fore foot strike percentages increase but do not overtake the rear foot strike preference (Hatala et al. 2013). A similar deviation from the fore foot strike pattern was noted for the Hadza of northern Tanzania in which males favor the midfoot and women and children favor rear foot. The shift to the rear foot strike is associated with increased running experience with age (Pontzer et al. 2014). Thus, the picture is very complicated in terms of biomechanical stress that may be operating on the heel due to frequency of activity, duration of activation, speed of running, and running substrate (e.g., hard or soft surface). The length of the calcaneal tuber (related to Achilles tendon moment arm length) is correlated to running economy (long calcaneal tuber = greater energy cost). In comparison to Neandertals, modern humans have shorter tuber lengths and more economical persistence running, which may have allowed better access to meat in hot environments (Raichlen et al. 2011). Dorsal spurs on the calcaneus are also

linked to increased activity (plantar spurs are linked to standing inactivity and excess weight) (Weiss 2012).

**Habitual activity and Tool use.** Mobility and subsistence are not the only physically taxing activities in the daily life of hunter-gatherers. Ethnographic data show that domestic economies such as tool making, child care and carrying, butchering/food preparation, textiles, and carrying firewood and water create physical strain (Bentley 1985; Cowlishaw 1981; Hurtado et al. 1985; Sahlins 1968). While the shift to increased reliance on tools is linked to evolutionarily more gracile bodies (Trinkaus 1983), these new activities left other tangible evidence of their impact on the body. For example, handedness appears to be rapidly skewed to the right in human populations and is strongly correlated with tool use (Cavanagh et al. 2016; Stock et al. 2013). Evidence from the Hadza (Cavanagh et al. 2016) and Aka (Robira et al.) suggests that handedness is strongest when making and using tools and comparative analyses suggest that the Hadza are less lateralized than modern populations, showing a mosaic progression for lateralization in use (Stock et al. 2013). Sex-based differences in increased upper limb robusticity has been identified in Australian hunter-gatherers and ethnographic data suggest it may be due to differences in tool use (Carlson et al. 2007). Unimanual activities (e.g., spear hunting, warfare) leave a distinct mark of directional asymmetrical in the upper limbs compared to bimanual activities such as grinding or rowing (Weiss 2009). While domestic economies vary across groups, they tend to be sex-based and more frequently involve lateralized repetitive stress compared to subsistence and mobility (Weiss 2009). Thus, the cultural context for a population is as important to upper limb lateralization and dimorphism as mobility patterns and running are to lower limb lateralization and dimorphism.

**Cultural Context for Windover Site and Factors Affecting Sex dimorphism**

The National Historic Landmark Early Archaic Windover Site (8BR46) dates to 9000-7929 BP calibrated and is located in east-central Florida, roughly eight kilometers west of Cape Canaveral. The Archaic Period (8000 to 1000 BC) is characterized by hunting-gathering subsistence economies with dietary staples including nuts, seeds, and shellfish; the end date varies regionally and relative to the advent of some form of plant/animal domestication (Milanich 1994). The Archaic Period in Florida follows the North American pattern (e.g., broad spectrum hunting, fishing, and plant gathering and use of freshwater resources) with subsistence weighted toward coastal shellfish and marine resource exploitation. The Early Archaic period (7500-5000 BCE) ushered in a comparatively wetter climate (Halligan et al. 2016), which created an abundance of resources and allowed population expansion with some examples of permanent sedentism; subsistence strategies were no longer dominated by big game and the broad spectrum foraging strategy that emerged is reflected in more complex tool kits (Doran & Dickel 1988b; Milanich 1994).

The Windover 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. The site was used as a burial ground with 5-6 short periods of activity,

peaking at 7450 BP, across 1000 years (Doran & Dickel 1988b). Mobility of the Windover population involved some seasonal travel within a constrained geographic area around the bog. The seasonality of use is indicated by analysis of preserved stomach contents which identified plants and fruits maturing during July and October. In addition, growth ring data recovered from the wooden stakes used to pin the burials in the bog indicated they were harvested in late summer/early fall (Doran & Dickel 1988a). Paleodietary analysis from carbon and nitrogen bone-collagen values and archaeobotanical information identified primary subsistence from river-dwelling fauna and terrestrial flora, such as grapes and prickly pear. Unlike most Florida Archaic populations, there was no extensive use of marine mammals or classic terrestrial fauna such as deer or rabbit (Tuross et al. 1994). Based on the seasonal occupations of the camp site and abundance of local resources, there is not likely to be a sex-based difference in lower limbs related to mobility, but foraging activities might create biomechanical pressure on weight-bearing bones of both sexes. A high incidence of upper body compression fractures is potentially the result of falls when crossing the rough terrain (Smith 2003). Prevalence of right rib compression fractures may result in tarsal asymmetry due to foot preference in balance during foraging.

The Windover population engaged in the typical egalitarian hunter-gatherer sex-based division of labor, as inferred from grave goods (artifacts buried with individuals). Grave goods include woven fabric (used to wrap the bodies for burial) and carved wood and bone tools (Adovasio et al. 2001; Doran & Dickel 1988a). The fabrics recovered from the bog were highly complex and labor intensive in their preparation (Adovasio et al. 2001). Analysis of the distribution of grave goods found statistically significant correlations between sex and age categories and functional category of artifact (e.g., hunting, weapons, domestic). Subadults had a significantly higher number of domestic artifacts (containers and bowls mainly) that were commonly associated with female adult burials and more grave goods (57%)—slightly more than adult males (55%) who received more grave goods than adult females (40%). Males and females were both found with hunting materials which suggest that both sexes engaged in the hunting of small mammals, reptiles, and fish; however, exclusively males were found with materials for hunting larger terrestrial mammals (e.g., atlatl components, spears, lithic projectiles). Males also were found consistently with hollow point awls which were used to make fishing nets.

Tool material also exhibited sex-based patterns with females using shells and males using stone, even though the final tool types were not the exclusive domain of one sex. Females were exclusively found with bird-bone tubes and turtle shells, possibly for the preparation of plant medicine; at least 13 plant-based medicines were identified in archaeobotanical analysis with three only found in the context of human remains (Tuross et al. 1994); hackberry for gynecological complaints (Herrick 1977; Speck 1941; Swank 1932; Vestal & Schultes 1939), black gum for a variety of treatments including intestinal (Boughman & Oxendine 2004) and chest complaints (Garrett 2003), and cabbage palm to treat headaches and reduce fevers (Brown 1994; Kniffen et al. 1994; Moerman 1998; Ottesen 1995). Further support for medicinal preparation is the clustering of mortar and pestle tools in subadult graves (which typically had female domestic artifacts). Females and subadults were also found frequently with butchered bone, which might indicate sex-

based food preparation activities (Adovasio et al. 2001; Hamlin 2001). The marked difference in subsistence activities—females engaging in a wide array of subsistence and tool economies, males engaging in hunting and some tool economies—suggests morphological differences may be found relative to labor.

Patterns of degenerative joint disease in Windover further elucidate possible activity wear (Smith 2008). Males exhibited a higher frequency of degenerative joint disease in the spine compared to females. The right elbow and shoulder had greater frequency of elements exhibiting signs of degenerative joint disease than the left and the wrist had very little degenerative joint disease. Females exhibited the most severe degenerative joint disease and female wrists, though, rare were more affected than males (only 1 male was affected in the wrist). Females exhibited significantly higher degenerative joint disease than males for the left sacro-iliac joint. Males were more likely than females to show degenerative change in the right and left knees, and rarely, in the ankle. The talus and calcaneus showed significant bilateral degeneration, which might reflect the biomechanical changes specific to running (Raichlen et al. 2011)and activity (Weiss 2012). Overall, males tended to have more evidence of degenerative change in the left and females in the right.

**Expectations**

1. Mobility
    a) Given the mobility pattern of the population and assumed lack of foot-wear, the weight-bearing tarsals will exhibit more robusticity than non-weight-bearing tarsals.
    b) Given the sex-based differences in the talus and calcaneus in previous research that suggests different mobility
        i. There will be between sex differences in weight-bearing bones.
        ii. There will not be between-sex differences in non-weight-bearing bones.
    c) Given the rib fractures from frequent falls, there will be asymmetry of foot bones reflecting foot preference. Based on degenerative joint disease patterns, there will be sex-based differences in lateralization.
2. Subsistence
    a) There will be a difference between males and females in carpal bones reflecting the sex-based division of labor.
    b) There will be lateralization of wrist bones reflecting handedness in complex tasks for making tools and textiles.

## MATERIALS

The Windover bog site (5,400m$^2$) is one of a number of Archaic period sites in Florida with underwater burials in peat; others include Little Salt Spring (6,800-5200 years ago) (Clausen et al. 1979), Republic Grove (Wharton et al. 1981), and Bay West (6840-5940 years ago) (Beriault et al. 1981 ). Graves were excavated from the soft peat around the edges of the pond and discovered during construction of commercial housing (Doran & Dickel 1988a). Roughly 100 were undisturbed burials with fully articulated bones; ages ranged from infancy to over sixty-five, with 52% classified as subadults (Purdy 1991).

Most individuals were buried in a flexed position, on their left sides, and with their heads toward the west. Bodies were pinned in their graves by sharpened stakes approximately 1m below the surface of the peat (Hauswirth et al. 1994) and interred within 24 to 48 hours after death (Doran 1992; Dickel 1988, Hauswirth 1991). Burials furthest from the pond edge at time of excavation dated to the earliest period of mortuary pond use and those closest, more recent. The nearly neutral pH of the pond (6.1-6.9) created ideal conditions for preservation of both skeletal and soft tissues (i.e. microscopically identified brain matter, preserved organic materials), which allowed researchers to sequence DNA from the brains (Hauswirth et al. 1994), reconstruct diet (Tuross et al. 1994), and study textile industries (Adovasio et al. 2001). Ancient mitochondrial DNA analysis suggests at least one matriline extending across the period of use (roughly 50 generations) and some spatial distribution of haplotypes, including the rare X haplogroup (Hauswirth et al. 1994).

The population exhibited predominantly good health and included individuals of extremely advanced age (50+) for hunter-gatherer groups; this likely reflects the resource abundance during deposition of the mortuary pond (Klingle 2006). But, common to hunter-gatherer populations, there were general health issues. Adults of both sexes exhibited a high incidence of osteoarthritis, which may result from a combination of advanced age as well as work-related biomechanical stress; osteoporosis was evident in older females (Smith 2008). Enamel defects were common in the population suggesting that childhood was a stressful period with regular interruptions to growth; those dying in childhood exhibited more growth interruptions than those surviving to 20 years old (Berbesque & Doran 2008; Berbesque & Hoover 2018). Twenty-two percent of individuals (including subadults) suffered some form of skeletal trauma, mostly in the ribs which might be attributable to falls when transporting goods or water over the rough and uneven terrain; fracture patterns indicate that some resulted from interpersonal violence (Smith 2003).

## 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. Three variables—length, width, and body height—were measured on four carpal and four tarsal elements (12 variables each); tarsal variables also include additional variables for the weight-bearing talus and calcaneus for a total of 16 tarsal variables (Table 1).

**Table 1: Measurements**

| Element | Measurement | Orientation | Description |
|---|---|---|---|
| Scaphoid | Length | proximal | scaphoid tubercle-lateral most point |
| | Width | palmar | bisection of scaphoid ridge |
| | Body height | proximal medial | bisection of scaphoid ridge |
| Capitate | Length | palmer | proximal-distal end |
| | Width | lateral | thinnest point |

| | | | |
|---|---|---|---|
| | Body height | lateral | inferior-superior facets |
| Lunate | Length | proximal | proximal-distal end |
| | Width | proximal | medial-lateral sides |
| | Body height | proximal | anterior-superior surface |
| Hamate | Length | lateral | proximal end-distal ridge (between metacarpal facets) |
| | Width | lateral | most medial to most lateral side of the facet |
| | Body height | distal | inferior most point to superior most point* |
| Calcaneus | Length | lateral | (Steele and Bramblett 1988) |
| | Width | superior | (Steele and Bramblett 1988) |
| | Body height | medial | at the calcaneus tuberosity |
| | 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) |
| | Body height | 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 |
| | Body height | distal | inferior-superior talar articular surface |
| Int. Cuneiform | Length | superior | proximal and distal midpoint |
| | Width | superior | thickest middle portion |
| | Body height | medial | inferior-superior |

Raw data were explored for significant outliers using Grubb's statistic and tested for the normal distribution. Due to morphological variation in trait size relative to the element, the natural log was taken for the between-sides average for each variable. Between-sex differences and differences between weight and non-weight bearing variables were tested via independent t-tests and univariate analyses. Lateralization was tested by directional asymmetry methods (Palmer 1994; Palmer & Strobeck 1986; Palmer & Strobeck 2003); for these data, the normal distribution was tested after univariate analysis to identify the presence of skew that might be affecting positive significant results. All results were evaluated relative to confidence intervals, power, and estimated effect size.

## 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 prior to testing for the normal distribution. Female variables were all normally distributed (Supplementary Table 1) except scaphoid length. Five male variables were not normally distributed (calcaneus body height, talus length, body height, trochlear tibia width and length). Descriptive statistics for trait size are found in Supplementary Table 2.

Given the mobility pattern of the population and assumed lack of foot-wear, we expected the weight-bearing tarsals would exhibit more robusticity than non-weight-bearing tarsals. The expectation (1a) is met (Table 2b-d, Figure 1); univariate analysis and independent samples t-test identified significant differences in tarsal bones when comparing weight-bearing (calcaneus and talus variables) to non-weight-bearing (navicular and intermediate cuneiform) bones. In the univariate analysis, there were significant differences but variances were not equal (Table 2a). An independent samples t-test (equal variances not assumed), however, confirmed a significant difference between weight-bearing and non-weight bearing bones ($t=-23.97$, $df=519$, $p=0.00$). The source of the unequal variance in the univariate analysis is the male sample (Table 2b). So, we conducted an independent samples t-test (equal variances not assumed), which identified significant differences between weight-bearing and non-weight bearing bones in males ($t=-19.76$, $df=337$, $p=0.00$). The results of the univariate analysis for females (Table 2c) also identified significant differences between weight and non-weight bearing bones; the power is high (100%) with a large estimated effect size ($\eta p=0.46$). A univariate analysis examining the entire set of tarsal bones identified a statistically significant between-sex difference, but with very low estimated effect size ($\eta p=0.01$) (Table 2d). When each tarsal element is examined individually for between-sex differences (Table 3a-d), the intermediate cuneiform (Table 3d) is the only significant result with high power (82%) and low-medium estimated effect size ($\eta p=0.18$).

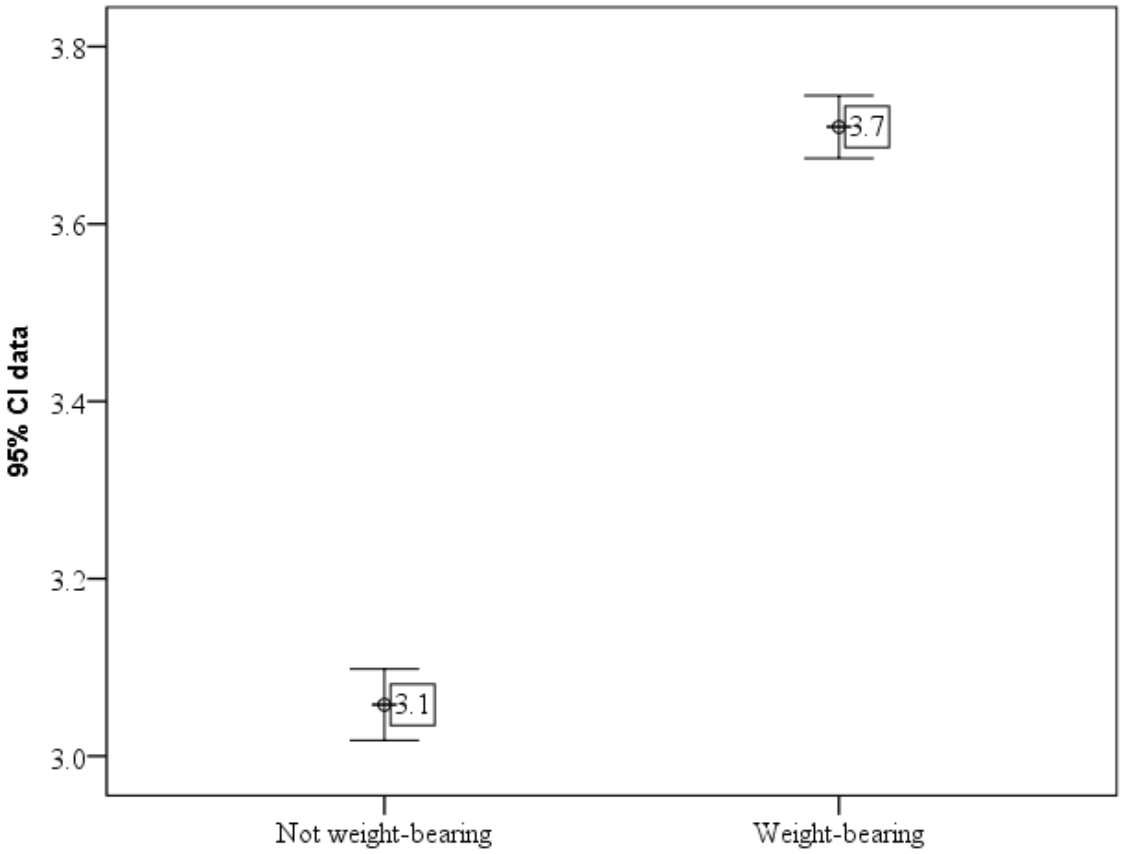


**Figure 1: Confidence intervals for the mean weight/non-weight bearing bones**

Given the sex-based differences in the talus and calcaneus in previous research that suggests different mobility, we expected there would be between-sex differences in weight-bearing bones. The expectation (1bi) is met (Table 2e-f); univariate analysis identified a significant between-sex difference in weight-bearing bones (Table 2e, Figure 3). We also expected there would be no between-sex differences in non-weight-bearing bones (Table 2f, Figure 3). The expectation (1bii) was met. For both results, the estimated effect sizes were low. Further, the power was low for the non-weight-bearing analysis (41%) which might mean a significant difference was not detected.

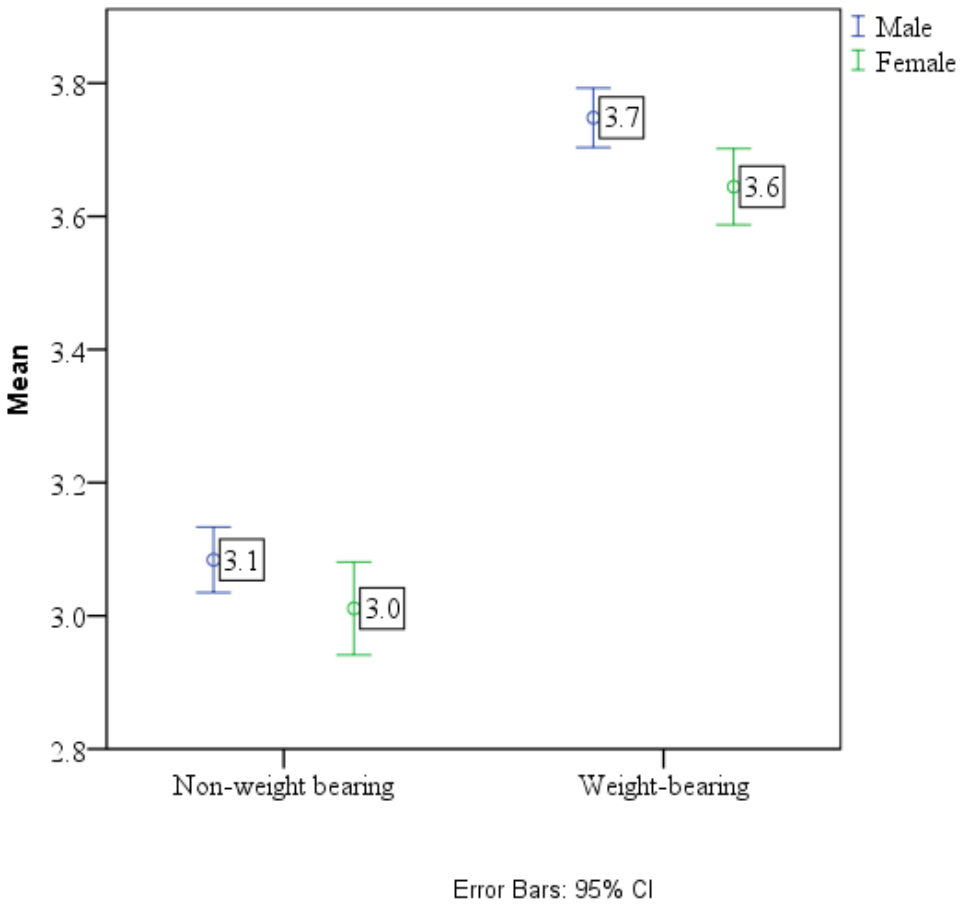


**Figure 2: Weight-bearing bones box plots**

**Table 2: Univariate Analysis of Mobility Expectations**

| | | | | | | | | | | | 95% CI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Levene** | **Sig** | **F** | **df** | **Sig** | **ηp** | **Obs Power** | **Mean** | **SD** | **n** | **Lower** | **Upper** |
| a | 7.04 | 0.01 | 538.69 | 1 | 0.00 | 0.47 | 1.00 | 3.47 | 0.46 | 600 | 3.43 | 3.50 |
| b | 5.82 | 0.02 | 363.27 | 1 | 0.00 | 0.49 | 1.00 | 3.50 | 0.46 | 379 | 3.45 | 3.54 |
| c | 0.74 | 0.39 | 186.24 | 1 | 0.00 | 0.46 | 1.00 | 3.41 | 0.45 | 221 | 3.35 | 3.47 |
| d | 0.37 | 0.55 | 4.66 | 1 | 0.03 | 0.01 | 0.58 | 3.47 | 0.46 | 600 | 3.43 | 3.50 |
| e | 0.64 | 0.42 | 2.98 | 1 | 0.09 | 0.01 | 0.41 | 3.06 | 0.31 | 225 | 3.02 | 3.10 |
| f | 0.08 | 0.78 | 7.92 | 1 | 0.01 | 0.02 | 0.80 | 3.71 | 0.35 | 375 | 3.67 | 3.74 |

a-weight bearing versus non-weight bearing bones in both sexes; b-weight bearing versus non-weight-bearing in males only; c-weight-bearing versus non-weight bearing in females only; d-between the sexes in tarsal bones; e-males versus females in weight-bearing bones only; f-males versus females in non-weight-bearing bones only

Given the rib fractures from frequent falls, we expected there would be asymmetry of foot bones reflecting foot preference. And, based on degenerative joint disease patterns, we expected a sex-based difference in lateralization. The expectation (1c) was not met. The directional asymmetry analysis did not indicate any lateralization of the foot bones, or 'footedness'. Based on descriptive statistics (Supplementary Table 3), tarsals are

slightly right dominant in 63% of variables in males and 56% in females. Overall, males tend to be less symmetrical with greater between-sides differences in 56% of the variables. The univariate sides-by-individuals analysis (Supplementary Table 4), however, only identified two lateralized variables (male intermediate cuneiform width and female talus body height), but these proved not significant after post hoc multiple test correction (Supplementary Table 5). Male cuneiform width was not normally distributed (Supplementary Table 1) which likely created a false signal for asymmetry and would have been either retested using the natural log or eliminated as problematic. Despite no significant presence of directional asymmetry, we compared male between-sides differences to female between-sides differences (Supplementary Table 6) in tarsal bones. There were no significant differences.

Given the sex-based division of labor inferred from grave goods, we expected there would be a between-sex difference in carpal bones. The expectation (2a) was met. The univariate analysis (Levene 1.280, Sig 0.259) identified significant between-sex differences in carpal bones (F=15.231, df=1, p=0.000). The observed power was high (97%) but the estimated effect size (ηp=0.05) was small. The 95% Confidence Interval of 2.74 ± 0.034 (2.71 to 2.78) excludes both the male mean (2.80) and the female mean (2.67). When each carpal element is examined individually for between-sex differences (Table 3), the lunate tops the list with high power (92%) and a low-medium estimated effect size (ηp=0.23). The hamate exhibited statistically significant between-sex differences but with lower power (59%) and small estimated effect size (ηp=.11).

**Table 3: Univariate analysis of individual elements**

| | | | | | | | | | | | **95% CI** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Levene** | **Sig** | **F** | **df** | **Sig** | **ηp** | **Obs Power** | **Mean** | **SD** | **n** | **Lower** | **Upper** |
| Scaphoid | 0.15 | 0.70 | 0.27 | 1 | 0.60 | 0.01 | 0.08 | 2.67 | 0.45 | 26 | 2.53 | 2.80 |
| Capitate | 0.91 | 0.35 | 1.92 | 1 | 0.17 | 0.05 | 0.27 | 2.78 | 0.27 | 16 | 2.70 | 2.87 |
| Lunate | 0.00 | 0.99 | 11.65 | 1 | **0.00** | **0.23** | **0.92** | 2.73 | 0.13 | 16 | 2.69 | 2.77 |
| Hamate | 0.60 | 0.44 | 4.97 | 1 | **0.03** | **0.11** | **0.59** | 2.87 | 0.19 | 26 | 2.81 | 2.93 |
| Navicular | 0.09 | 0.77 | 0.59 | 1 | 0.45 | 0.02 | 0.12 | 3.24 | 0.35 | 42 | 3.13 | 3.35 |
| Calcaneus | 0.01 | 0.93 | 0.30 | 1 | 0.59 | 0.01 | 0.08 | 3.78 | 0.49 | 26 | 3.62 | 3.93 |
| Talus | 0.15 | 0.70 | 2.41 | 1 | 0.13 | 0.06 | 0.33 | 3.69 | 0.21 | 16 | 3.62 | 3.75 |
| Int. Cuneiform | 0.13 | 0.72 | 8.71 | 1 | **0.01** | **0.18** | **0.82** | 2.88 | 0.12 | 42 | 2.84 | 2.92 |

Given the previously reported handedness in hunter-gatherers that are regularly engaged in complex tasks (e.g., tool-making, textile making), we expected there would be a lateralization of wrist bones. The expectation (2b) was not met. The directional asymmetry analysis did not indicate any lateralization of the hand bones. Descriptive statistics (Supplementary Table 3) indicated some side preference: male carpals are evenly split between right and left but female carpals exhibit right dominance (7/12 variables). The univariate sides-by-individuals analysis (Supplementary Table 4), however, did not identify significant directional asymmetry in any variable. Despite no significant directional asymmetry, we compared male between-sides differences to

female between-sides differences in each carpal bone (Supplementary Table 6). There were no significant differences.

## DISCUSSION AND CONCLUSION

**Mobility.** The archaeological analysis suggested that Windover population lived in a resource rich riverine area but unlike many other Florida Archaic populations (Milanich 1994), they did not did not exploit high levels of marine animals. Based on archaeological data, their residential mobility was inferred to be low (Doran & Dickel 1988a; Doran & Dickel 1988b). Further, the warmer climate during the Archaic ushered in a subsistence shift from big-game hunting (as megafauna migrated north) and to broad spectrum foraging (Doran & Dickel 1988a; Halligan et al. 2016). Given the rough terrain and high activity levels inferred from prevalent degenerative joint disease (Smith 2008), we expected significant differences in weight-bearing tarsals compared to non-weight bearing tarsals (Expectation 1a). The results were consistent with this expectation. The mean for the non-weight-bearing bones (3.06) and the mean for the weight-bearing bones (3.71) fall well outside the lower and upper error margins (respectively) of the confidence interval for the total tarsal sample (Table 2a and Figure 2), suggesting a strong biological difference between the two sets of bones. Thus, we can conclude that weight-bearing activities influenced greater robusticity in weight-bearing bones.

The intermediate cuneiform exhibits significant between-sex differences. The female data are the source of the significant variation, with means positioned below the lower error margin (body height) or at the error margin (length and width) for the 95% confidence interval (Supplementary Table 2 and Figure 1). Anatomically, the intermediate cuneiform articulates with the navicular proximally and second metatarsal distally. The second metatarsal-intermediate cuneiform is a highly stable joint with limited mobility. As a keystone tarsometatarsal joint (one of the five, also called Lisfranc’s joint), any stresses (from biomechanical to fracture or dislocation) rarely occurs without implicating the second metatarsal base (Liu et al. 1997). The second metatarsal receives some of the highest peak pressure during locomotion and at rest—this is particularly pronounced in barefoot locomotion (Rodgers 1988):1826. Injury to Lisfranc's 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. Even non-severe falls can cause injury to the joint and result in degenerative arthritis as a sequalae to articular cartilage damage caused by injury (Liu et al. 1997). While we cannot test the cause of this significant between-sex variation, the anatomically implications are clear: activity and trauma influence the joint, particularly when barefoot.

Given the differences in subsistence and domestic economies between males and females that might differentiate type of habitual locomotor substrate (e.g., females preferring shell tools and males preferring stone tools, females engaged in preparation of medicine) and previously identified differences in degenerative joint disease in the talus and calcaneus (Smith 2008), we expected sex-based differences in weight-bearing bones (Expectation 1b). The results were consistent with this expectation; there were significant differences between the sexes with high power and large effect. The t-test results for males indicate the same result as the univariate analysis for males; thus, the inequality of male variance

does not seem to have reduced the robusticity of the between-sex univariate analysis of differences in weight-bearing and non-weight-bearing bones. The high power across three tests and the large estimated effect size suggest a robust biological difference. Perhaps more tellingly, there are no differences between the sexes in non-weight-bearing bones; but, the power is low (41%) so a significant result may have gone undetected. The confidence interval data suggest the lack of significant between-sex difference in non-weight-bearing bones is valid because weight-bearing means for both sexes fall outside the confidence interval for the total sample but non-weight-bearing means lie within the confidence interval. And, the estimate effect size is extremely low but the sample large.

The intermediate cuneiform was the only tarsal bone significantly different between sexes (when each element was examined individually). Perhaps its implication in locomotion via articulation with the second metatarsal is a factor in what might be an undetected significant difference in non-weight-bearing bones (due to low power). Either way, we can conclude that weight-bearing activities influenced between-sex morphological variation and perhaps non-weight bearing bones are implicated in weight-bearing activities via anatomical articulations across the foot. A point of speculation might be that females navigated a wider range of terrains than males (given their preference for shell tools) or might have foraged for a greater diversity of raw materials (for plant-based medicines or textiles). Taken in light with the previous discussion on the intermediate cuneiform and bone fractures due to possible falls (Smith 2003), there may well be some sex-based activity difference and even difference in the local substrate where each sex forages or in locomotion patterns associated with particular foraging activities.

The fracture analysis from previous research suggested a hazardous terrain—regular logistical mobility in foraging, hunting, and gathering raw materials for domestic economies were implicated as the potential source for the rib fractures, which tended to be on the right side (Smith 2003). Further, sex-based lateral differences in degenerative joint disease (males, left; females, right) in the talus and calcaneus (Smith 2008) led to the expectation that this might be the long-term outcome of foot preference and be manifest in directional asymmetry of weight-bearing bones (Expectation 1c). There was no significant directional asymmetry (as a proxy for lateralization due to foot preference). While males tend towards greater between-sides differences than females, females have a much larger between-sides difference in two important measurements: calcaneus length and load arm length. These variables are implicated in running (Raichlen et al. 2011) and other physical activities (Weiss 2012) but we cannot draw any conclusions about what this might mean without a comparative sample in which to contextualize the data. Ultimately, the results of the analysis indicate that there is no evidence for favoring a particular foot due to injury or foot preference ("footedness").

**Subsistence.** We hypothesized that there would be a difference between males and females in carpal bones reflecting the sex-based division of labor and this was upheld and with a large estimated effect size (Expectation 2a). Between-sex differences in carpal bones suggests sex-based differentiation of tasks that influenced morphology. The lunate is particularly interesting given its high power and medium effect size; anatomically, the

lunate articulates with the radius and is marked by the large articular facet covering most of its proximal surface that is implicated in hand rotation. Differential use wear in repetitive tasks may have shaped morphological differences in this bone. The difference in tool types (shell for females and stone for males) and activities may contribute to variation in wrist bone size. Female means lie just below the lower margin (body height) or at the lower error margin (length and width) of the 95% confidence interval, while male means all lie within it toward the upper error margins (Supplementary Table 2). Female body height and length fall below the lower margin of the confidence interval and width lies at the lower error margin while male means all lie within it (Supplementary Table 2). This suggests that females are significantly different. Whether this reflects female task specialization or more robust wrists in males due to hunting activities can only be speculated, given the available data and archaeological context.

We expected that hand bones would exhibit asymmetry due to handedness in tasks (Expectation 2b) (Cavanagh et al. 2016; Maki 2013; Robira et al.). This hypothesis was not upheld. As with the feet, there were no significant variables exhibiting directional asymmetry. This was surprising given the intricate and taxing work involved in making textiles and the wide array of tools used by both males and females; further, the lateralized degenerative joint disease in male shoulder and elbow regions (Smith 2008) and evidence for spear-throwing in males (tools found exclusively associated with male graves) led to an expectation we might see lateralization in male carpal bones. But, as suggested by Maki (Maki 2013):238, the wrist is a complex system in which small changes in the anatomy of one bone be offset by changes in other aspects of the anatomy.

The most statistically robust results (when considering p-value alongside power, effect, and confidence intervals) are for differences between weight-bearing and non-weight-bearing bones and for sex-based differences in carpals. The rough terrain traversed by the Windover population may have left them vulnerable to falls and compression fractures resulting from those falls (Smith 2003). This also may have been formative in biomechanical pressure on the weight-bearing bones of the talus and calcaneus, enlarging them relative to other bones. As the analysis was conducted on scaled trait size (natural log of between sides averages), the difference in absolute bone size is not a confounding factor.

Overall, we can conclude that there are significant differences between-sex differences but some might attributable to normal sex dimorphism. Still, archaeological evidence for sex-based division of labor and the robust findings for sex-based differences in the carpals suggests culturally-based morphological influences as well. And, the significant differences in weight and non-weight-bearing bones across the sample and within the sexes suggests a mobility component to morphology. The Windover population is not remarkable in their morphology compared to other hunter-gatherer groups, and while we might have expected some lateralization due to strong handedness in specialized tasks (Cavanagh et al. 2016; Robira et al.), hunter-gatherer handedness is not as pronounced as in industrial societies (Cavanagh et al. 2016) nor is sex dimorphism (Wolfe & Gray 1982). 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. However, without expectations or hypotheses derived from ethnographic information, archaeology can only be descriptive.


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