

**LATERALITY AND HANDEDNESS:
ANALYSIS OF CROSS-SECTIONAL GEOMETRY IN ARCHAIC POPULATIONS**

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Abstract

Laterality, or the tendency of a population to use one hand over the other in a variety of actions, is a unique, panspecies trait in humans. This tendency is argued to indicate a more profound structural asymmetry that extends to cerebral function; lateralization of the brain and body has impacts on a range of human characteristics, from material culture to language. To analyze the handedness of past populations, researchers rely on morphological and biomechanical asymmetries present in skeletal remains, specifically in the diaphyses of long bones. Previous research demonstrates that humans show a strong right-hand bias and greater overall asymmetry in the upper limb, including in the hands themselves. However, studies of the laterality of hand bones have been limited to the second metacarpal.

This study evaluates directional bilateral asymmetry of the hand using the second through fifth metacarpals. These are measured from a sample of 50 adults from Middle and Late Archaic forager groups buried at three sites in western central Tennessee. Based on the well-established right-biased asymmetry for humans, this sample was expected to show right directional asymmetry. Cross-sectional properties obtained for these individuals were analyzed for magnitude and direction of asymmetry—given by percent directional asymmetry (%DA) and percent absolute asymmetry (%AA)—as well as for the overall shape of the cross-section, which should be rounder in the dominant hand. Results indicate little sexual dimorphism among the metacarpals and predictable trends of increasing asymmetry in the medial palm. This study cautions against using the cross-sectional properties of a single metacarpal to estimate those of the rest and highlights the need for further research in this area to establish and understand patterns of asymmetry across the metacarpals.

Keywords: asymmetry, handedness, metacarpals, Archaic humans, cross-sectional geometry

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CHAPTER 1: INTRODUCTION

Laterality, known as “handedness,” or the tendency of a population to preferentially use one hand in a variety of actions, has long been a subject of scientific inquiry. Skeletal evidence of directional asymmetry has been argued to indicate a more profound structural asymmetry extending to cerebral function, impacting material culture and language. Furthermore, its evolutionary relevance is continuously debated. While origins of laterality are undetermined, most researchers posit that handedness is a uniquely human trait while others argue that there is evidence for laterality among non-human primates as well (Lazenby, 2002a; Schultz, 1937).

Asymmetrical behaviors should have asymmetrical consequences on skeletal structure; that is, skeletal remodeling patterns, especially in the diaphysis, should reflect the predominant use of one limb over another. Initiated by increased mechanical stress, remodeling strengthens bone through changes to its mass and density (Ruff et al., 2006; Martin et al, 1998). Prior research has found that the upper limb tends to reflect asymmetric loading more than the lower limb (Auerbach and Ruff, 2006). Furthermore, long bone diaphyseal breadths have been shown to most clearly indicate this laterality (Trinkaus et al., 2004), with respect to long bone lengths and articular size (Auerbach and Ruff, 2006). These patterns have been established in the second metacarpal as well, using the trabecular structure and cross-sectional geometry of the second metacarpal to signify handedness (Lazenby, 1998a, 1998b; Lazenby et al., 2008).

This thesis evaluates the directional asymmetry of the second through fifth metacarpals of forager groups from the Middle and Late Archaic populations buried in three sites in western central Tennessee. Previous research has focused almost exclusively on the second metacarpal; this study observed the second through fifth metacarpals to determine if patterns in directional

asymmetry are evident and consistent across the hand. Laterality was analyzed using cross-sectional geometry of the middle diaphyses of metacarpals, which approximates the biomechanical strength properties in bending and torsion. Dimensions were converted to percent directional asymmetry (%DA) to evaluate magnitude and direction of asymmetry and percent absolute asymmetry (%AA), which indicates total asymmetry present in a given dimension.

BACKGROUND

Population-wide bilateral asymmetry in humans has long been a research focus, in part because it is so unusual; the human body is, by and large, bilaterally symmetrical, but notable asymmetries exist, especially with regard to upper limb use preferences (Auerbach and Ruff, 2006 and the papers cited in their appendix). While some are random fluctuating asymmetries that vary by individual, others are fundamentally side-biased—these are cognitive and mechanical asymmetries whose directional bias persists across a population (Corballis, 2009). One of these profound asymmetries is laterality, or “handedness,” which refers to a population-wide bias towards one side of the body for a variety of tasks; on the contrary, “hand preference” refers to favoring one hand over another on a task-by-task basis (Lazenby, 2002c). Population-wide hand-bias is one of the most promising sources of information about cerebral asymmetry, as it is the most obvious physical manifestation of laterality. While the brain typically exhibits bilateral symmetry for most functions, some tasks are asymmetrical; for example, it is generally accepted that the production of speech is lateralized in the left hemisphere (Corballis, 2009). Moreover, some theories posit that speech developed directly from manual gestures, a process that inextricably links the hands with speech pathways in the brain (Corballis, 2003). Thus, the

evolutionary, cultural, psychological, and neurological implications of human laterality have generated considerable interest in this area of study.

Laterality in Humans

While cerebral asymmetry and even hand preference is hardly unique to humans, handedness itself appears to set humans apart as a species (Corballis, 2009; Schultz, 1937; McGrew and Marchant, 1997; Byrne and Byrne, 1991), though this assertion is not without contention. Some scientists claim a right-hand bias has been observed in several species of non-human primates (Hopkins et al., 1993; Westergaard and Suomi, 1996). However, in a study of wild chimpanzees in Tanzania, McGrew and Marchant (2001) found little evidence for systematic hand preference in the wild, positing that any hand preference observed in captive non-human primates is the result of contact with humans, either thanks to mimicry or to the artificial nature of tasks in a captive environment, rather than overarching population-wide handedness. The evolutionary origins of this uniquely human trait remain unclear, though it has been suggested that tool complexity played a role in its development. Some have proposed that hand preference was reinforced as tool manufacture and use required bimanual recruitment (Frost, 1980; Uomini, 2009); consistently using one hand in the primary task produces better results (McGrew and Marchant, 1999), though whether this advantage was great enough to produce a population-wide right-hand bias is unclear.

Sources of Laterality in the Postcranial Human Skeleton

Not only are humans unique in their preferential use of the right limb, but this bias influences human long bone dimensions, forming the basis for investigations into human

bilateral asymmetry. The greater directional asymmetry documented in upper limb long bone dimensions is especially notable with respect to the general lack of bilateral asymmetry in the lower limb. Closely associated with body mass, the lower limb is constrained to symmetrical loading and use by its role in weight bearing during locomotion (Ruff, 2000). The lower limb does show evidence of a left bias (Auerbach and Ruff, 2006; Schultz, 1937), though it is minor.

The first appearance of these patterns of bilateral directional asymmetry in humans is unclear. Auerbach and Ruff (2006) used a global sample of human skeletal remains to demonstrate that populations throughout the Holocene show both the previously described upper limb and lower limb patterns of directional asymmetry. Other researchers have demonstrated evidence for bilateral directional asymmetry of the upper limb in Neandertals and Pleistocene anatomically modern humans (Churchill and Formicola, 1997; Trinkhaus et al., 1994).

Experimental archaeological techniques suggest greater temporal depth, estimating that tool manufacturing was lateralized by 1.4-1.9 million years ago (Toth, 1985). However, in their review of material culture and handedness in the archaeological record, Steele and Uomini (2005) were careful to note that Toth's (1985) methods were narrowly applicable. While they contended that the material evidence for lateralized behavior in our hominin relatives is sparse (and specious), they agreed that the archaeological record does suggest lateralized behavior in anatomically modern humans, consistent with Auerbach and Ruff's (2006) findings.

Changes in bilateral asymmetry associated with subsistence practices are well established (Auerbach, 2007; Auerbach and Ruff, 2006; Bridges, 1989; Bridges et al., 2000). Globally, bilateral asymmetry of the upper limb decreased over time as subsistence practices progressed from foragers to horticulturalists to agriculturalists, presumably because mechanical demands changed with new food processing methods, mechanically advantageous tools, coupled with

decreases in mobility and increases in sedentism (Auerbach, 2007; Ruff, 2005). Importantly, although the degree of asymmetry decreased, the frequency of right directional asymmetry is retained across space and through time despite subsistence (thus, behavioral) changes (Auerbach and Ruff, 2006).

The Archaic foragers of western central Tennessee used in this study were a seasonally sedentary population that utilized freshwater resources (Bissett, 2014). According to prior research, the greatest amount of asymmetry and sexual dimorphism in the upper limb was present in the early Holocene among pre-industrial individuals; asymmetry was significantly right-biased, with males demonstrating more asymmetry than females (Auerbach and Ruff, 2006; Ruff and Jones, 1981). Thus, Archaic males from Tennessee could be expected to show significantly more asymmetry than females from the same population. Moreover, the primary goal of this study is to evaluate asymmetry across the palm; because foragers have been shown to demonstrate the greatest amount of asymmetry of any subsistence group, their metacarpals are more likely to show this asymmetry if it exists. A more thorough understanding of the reflection of biomechanical loading in the skeleton, and its application to understanding the mechanics in the hand, is reviewed below before further discussing the expectations of this study.

Biomechanics and Cross-sectional Properties

Investigations of skeletal asymmetry rely on biomechanical and morphological asymmetries to infer lateralized mechanical loading and behaviors. It is presumed that the dominant limb is subject to a greater magnitude and wider variety of strains and is therefore stronger in all dimensions. The driving force behind these investigations is the theory of bone functional adaptation (Cowin et al., 1985), which defines the relationship between skeletal

structure and function. This theory states that bone is remodeled (deposited and absorbed) in response to mechanical forces in order to optimize the balance between size and strength (Ruff et al., 2006). Bone is plastic in response to loading; modeling and remodeling processes react to changing mechanical demands and environments, even in adulthood after the termination of primary longitudinal growth (Ruff et al., 1994; Trinkaus et al., 1994). A bone that is strong enough to withstand external forces of loading yet light enough for efficient mechanical movement is considered to be optimally adapted.

As mentioned, remodeling processes are integral to achieving this optimal adaptation. Bone strength depends on the maintenance of bone mass to withstand routine stresses, which occurs when bone formation and resorption are balanced: old bone is replaced with new bone matrix in a 1:1 exchange. If formational processes are more active, the bone's mass will be inefficiently large; if resorptive processes are more active, the bone will be too light to withstand loading without fracture.

The above relationship simply outlines the process of bone mass conservation—the model gains additional components when increased loading demands that the bone adapt to withstand new stresses. Mechanical loading stimulates the cortical bone to remodel through periosteal apposition, redistribution of bone about the centroid, and osteonal remodeling (Currey, 2002). These reactions to stress indicate that cortical bone morphology is correlated with the mechanical demands acting on bone, and therefore may be used to infer the kinds of tensile and compressive stresses to which the bone was subject.

However, these remodeling processes do not respond uniformly throughout cortical bone due to functional constraints and differential plasticity. For example, articular surfaces are typically canalized and developmentally restricted; despite considerable mechanical loading,

external articular dimensions show no significant increase in surface area (Lieberman et al., 2001; Ruff, 2005). Likewise, long bone length is also highly conservative, demonstrating even less asymmetry than articular surfaces (Auerbach and Ruff, 2006). Long bone diaphyseal breadths, in contrast, have been shown to be reliable indicators of activity (Trinkhaus et al., 2004). Cross-sectional properties of long bone diaphyses, therefore, provide valuable information about patterns of loading and activity for a given individual. Although metabolic forces and genetic factors also contribute to bone remodeling, the strength properties of long bone diaphyses have proved responsive to specific mechanical stimuli (Ruff et al., 2006) and are generally good indicators of habitual behavior and asymmetrical loading (Shaw and Stock, 2009a, b; Jones et al., 1977; Jaworski et al., 1980). The quantity and distribution of cortical bone, then has been the focus of researchers seeking to understand the effects of activity in and evidence for past behavior from the long bones of the limbs.

In light of these previous studies, the long bone diaphysis potentially reveals valuable information about mechanical loading through analysis of its cross-sectional properties. These biomechanical properties are determined using engineering beam theory to model the response of bone to various mechanical strains. Cross-sectional properties calculated this way take into account the distribution of material within a bone to determine its strength (Ruff, 2003). Viewed as a hollow beam, the cross-sectional properties of bone are used to determine its resistance to axial loading, bending, and torsional forces (Ferretti et al., 1996). Bone, like other materials, resists greater loads when it is placed farther away from the neutral axis around which bending occurs (typically near the centroid, but see Lieberman et al., 2004). Total area (*TA*) roughly reflects this relationship, and gives the size of the cross-section, while cortical area (*CA*) indicates the distribution of material in the diaphysis, especially relative to *TA*; larger *TA* and

smaller CA indicates a thinner cortical wall distributed farther from the centroid of the cross-section. These areas are proportional to the bone's axial strength—its ability to withstand tensile and compressive forces—and are increased by periosteal apposition and endosteal resorption (Ruff et al., 1994).

Most mechanical loading involves some combination of compressive and tensile forces, resulting in bending. The bone's bending strength (rigidity) is quantified using the second moments of area (I), which estimate the bone's resistance to bending about a neutral axis (where the amount of stress or strain equals zero) by taking into account cross-sectional area and the distribution of bone within the section. I_x and I_y , referred to in this work as I_{ml} and I_{dp} (I_{ap} is used to refer to I_y in relation to the radius), estimate bending strength in the dorsopalmar/anteroposterior and mediolateral planes, respectively. I_{ml} represents the x-axis and measures bending rigidity when the bone is bent dorsopalmarly. I_{dp} represents the y-axis and likewise measures the bone's bending rigidity when bent mediolaterally. The maximum and minimum bending rigidities of bone are designated by I_{max} and I_{min} , and their locations vary based on the diaphyseal shape. The polar second moment of area (J) approximates torsional strength and, as the sum of any two perpendicular values of I , gives a good estimate of overall bending rigidity.

Metacarpals and Handedness

The second metacarpal (MC2) is a tubular bone that preserves well in the archaeological record; as such, it has been the focus of extensive study, elucidating growth and development, stature, sex, bone loss, and pathology in forensic and archaeological contexts (Lazenby, 2002b, 2002d; Glencross and Agarwal, 2010; Case and Ross, 2007; Lazenby et al., 2008). Because the

metacarpals are tubular bones, the basic assumptions about the behavior of the long bone diaphyses in response to mechanical loading (outlined above) persist in the diaphysis of the second metacarpal, and hand dominance has been assessed using the cross-sectional properties and trabecular architecture of MC2 (Lazenby et al., 2008). Biomechanical investigations of the hand bones have been somewhat limited thus far, however, observing primarily (if not exclusively) the second metacarpal. Garn et al. (1991) compared the correlations of the bone areas of the second, third, and fourth metacarpals to stature and body mass and argued that for these size relationships and patterns in age-related bone loss, a single metacarpal predicts trends as well as any other. Interestingly, although this study is cited to justify biomechanical research focused solely on the second metacarpal (Lazenby, 1998a), it did not evaluate either directional asymmetry or cross-sectional properties.

Until the mid-nineties, evaluations of handedness based on the second metacarpal produced a preponderance of evidence in support of a systemic right-hand bias among human populations (Plato et al., 1980; Garn et al., 1976). However, unlike previous studies that had focused solely on the cross-sectional area of the bone, Roy et al (1994) investigated the biomechanical properties of MC2 and found that dominance, regardless of the side, showed increased dimensions in total area and second moments of area. This study also made important observations about metacarpal movement and bone deposition, namely that handedness extends beyond finger flexion; the dominant hand should be strengthened in both the mediolateral and the dorsopalmar planes, resulting in a rounder cross-sections to resist multi-directional loading. Roy et al. (1994) noted that analyses of grip strength for handedness are meretricious and must be handled carefully, because grip strength only measures digital strength in flexion (in the

dorsopalmar plane). Of course, metacarpals normally experience loading dorsopalmarly, and are therefore more likely to be strengthened along this axis.

The implications of this observation have been interpreted differently, however. Lazenby (1995) posited that precisely because of this loading relationship the second metacarpal of the dominant hand should be non-circular, maintaining that increased finger flexion in the dominant limb should result in greater dorsopalmar strength. He argued that laterality studies using radiogrammetry should not use formulae based on a circular model, lest their results underestimate strength properties. However in his 1998a publication, Lazenby revised his earlier stance, finding that the circular model for radiogrammetric studies actually produces less error than the elliptical model. This suggested that the metacarpals of the dominant limb should indeed have a more circular cross-section.

The study presented herein evaluates the second through fifth metacarpals for evidence of dominance across the palm, and to understand the patterns of asymmetry that occur within the hand across the digital ray, in light of this previous evidence. The thumb (the first metacarpal) was excluded from this study, as its movements are vastly different from the other metacarpals and would therefore complicate the analysis. The metacarpals (again, with the exception of MC1) are mechanically stable within the hand, with limited motion. The carpometacarpal joints experience greater freedom moving across the palm from MC2 to MC5, but their primary motion is flexion during grasping (Palastanga and Soames, 2012). Thus, it is expected that all metacarpals to be strengthened dorsopalmarly, regardless of hand dominance. This departs from the usual thinking in terms of lateral asymmetry; typically, deviation from diaphyseal circularity indicates limb dominance (Lazenby, 2002c). This logic holds true with long bones, such as the radius. Radii have more mechanical freedom than the metacarpals, whose movement occurs

primarily in a single plane, and unlike the metacarpals they are recruited for repetitive loading and power tasks (such as lifting, throwing). Thus, a round radial cross-section would indicate that the bone was not subject to as much mechanically-induced remodeling; the dominant limb should have a less round diaphyseal shape.

Also relevant to this particular sample is the articulation between laterality and tool manufacturing. Marzke and Shackley (1987) used experimental archaeology to evaluate the types of grips used during tool manufacturing and concluded that the process relied primarily on a precision grip rather than a power grip. A precision grip includes the use of the thumb and one or more fingers (usually the second or third), with or without the passive recruitment of the palm in support. A power grip includes using the fingers or the fingers, thumb, and the palm to strongly squeeze (Marzke, 1997). The reliance on the precision grip during flint-knapping indicates that the palm is not actively engaged during tool manufacture, thus it is likely that the laterality of this important fine motor task will not be reflected in the cross-sectional strength properties of the metacarpals.

In consistently side-biased individuals, both strength and fine motor tasks are performed with the same hand; only a few (left-handed) individuals deviate from this, using one hand for strength tasks and the other for fine motor skills (Lazenby, 2002c). This more or less stable coupling of grip and fine motor tasks in the dominant limb, combined with Lazenby's (1998a) and Roy et al.'s (1994) findings regarding diaphyseal circularity, would seem to suggest that while grip strength alone produces an elliptical cross-section, the dominant hand would more likely have rounder metacarpal diaphyses.

GOALS AND EXPECTATIONS

Though inquiries into laterality have been ongoing for many decades, there is a notable absence of literature on the metacarpals' abilities to indicate handedness. Previous research into the biomechanical properties of the hand has largely neglected most of the palm, prioritizing instead the second metacarpal. While evidence suggests that handedness can be determined from the diaphyses of metacarpals, scientific inquiry has yet to corroborate this hypothesis with the third, fourth, and fifth metacarpals. This study seeks to address this question, evaluating the second through fifth metacarpals for evidence of laterality across the hand.

As reviewed above, metacarpals normally experience mechanical loading primarily in the dorsopalmar plane; therefore, all metacarpals should demonstrate more periosteal apposition along the dorsopalmar (DP) axis rather than the mediolateral (ML) axis. However, increased reliance on the dominant hand for a variety of tasks should result in a rounder cross-section of these metacarpals; the ratio of the second moments of area (I_{ap} and I_{ml}) should approach 1. Research has shown a profound right-biased asymmetry in humans, particularly in the upper limb, therefore it is likely these individuals will also exhibit right directional asymmetry (Auerbach and Ruff, 2006; Lazenby et al., 2008). Furthermore, previous studies have established that forager populations have the greatest magnitude of directional asymmetry, as well as the most sexual dimorphism in this respect (Auerbach and Ruff, 2006; Wescott, 2006; Trinkaus et al., 1994). This suggests that laterality and sexual dimorphism should be observable in the second through fifth metacarpals in this sample of foragers, assuming the sample is sufficiently large. Samples from each site were pooled, as it has been recognized that these samples are temporally and demographically comparable (Herrmann, 2002; Bissett, 2014) and therefore unlikely to demonstrate significant differences.

This thesis, then, seeks to investigate the directional asymmetry present across the palmar arch using a sample of Archaic individuals. The following chapter describes the archaeological sample, methods of data collection, statistical analyses, and limitations of this work. Chapter 3 reports the results, followed by the analysis of these results, conclusions, and recommendations for further research in Chapter 4.

CHAPTER 2: MATERIALS AND METHODS

This chapter details the skeletal materials used in this study and the methods of data collection and statistical analyses employed to address the questions posed in Chapter 1. *The Archaeological Sample* describes the skeletal remains, site history, and limitations, while descriptions of techniques and analyses are under the section labeled *Analytical Methods*.

THE ARCHAEOLOGICAL SAMPLE

The sample used in this study was comprised of 50 individuals (28 males, 22 females) from each of the three Archaic sites: Eva, Cherry, and Ledbetter Landing. These skeletal remains are housed in the McClung Museum of Natural History and Culture at the University of Tennessee in Knoxville, TN. Only adult males and females were used for this research; individuals were selected and demographic information used in this study was based on records maintained by the McClung Museum. This information was obtained from the most recent inventory, which was produced from Maria Smith's 1990 assessment of the collections at the museum. The radii and metacarpals 2, 3, 4, and 5 on both the left and the right sides of each individual were analyzed where available. Elements chosen were paired (meaning both the left and the right were available for study), had intact midshaft diaphyses, were free from pathology, and were generally complete enough to measure with the osteometric boards and calipers (exceptions are discussed in the "*Limitations*" below).

The thumb (metacarpal 1) was excluded as its movement is not directly comparable to that of the other metacarpals; thanks to its opposition, MC1 should be strengthened through periosteal deposition along the AP and ML axes regardless of handedness, thus its laterality would present differently in biomechanical analysis. The radius provided a comparison for

laterality; the forearm undergoes different mechanical loading than the hands, recruited for many other actions (such as lifting). Laterality observed in the radius, though it may present differently from that in the metacarpals, should still reflect directional asymmetry in the population and is therefore a good check on the metacarpals' analytical abilities.

Site History

The Archaic period in North America began at the end of the last Ice Age (approximately 10,000 BP) and lasted through the Altithermal and Medithermal periods (approximately 1150-1200 BP) before giving way to the Woodland period (Lewis and Kneberg, 1958; Browman et al., 2013). This period was characterized by pre-agricultural, pre-ceramic populations that were nomadic to semi-sedentary, and that primarily subsisted by foraging (Browman et al., 2013). In the Archaic North American Southeast, forager groups exploited freshwater resources as well as the small and medium-sized game and wild flora of the eastern woodlands. This subsistence strategy required significant mobility and relied more heavily on manual labor than later, more sedentary horticultural and agricultural practices. It is expected that this routine dependence on the hands for a variety of subsistence tasks had biomechanical implications; experiencing daily strain caused bone to respond and strengthen accordingly. The expectation is that this consistent, intensive hand use resulted in enough bone remodeling that hand preference will become apparent with the analysis of the diaphyseal cross-sectional properties of the metacarpals, as the dominant hand would have been exposed to the greatest strain.

The Eva site (40BN12) dates to the Middle and Late Archaic and is located in Benton County, Tennessee, west of an expanse of marshy land known as Three Mile Slough. Nineteen individuals from this site were examined for this research (9 males, 10 females). During its

occupation, the site was located near water channels that provided abundant freshwater resources for Archaic foragers to exploit and discard, producing shell middens where humans, canines, and trash were buried (Lewis and Kneberg, 1958; Lewis and Lewis, 1961). The University of Tennessee excavated this site in 1940, sponsored by the TVA (Lewis and Lewis, 1961). The Eva shell mound is divided into five strata and dates as early as 8900 cal BP (Bissett, 2014). Eva I, comprised of strata IV and V, represent the site's earliest occupation, followed by Stratum III, wherein a sparse evidence of occupation indicates a brief period of disuse. Stratum II is designated Eva II, which corresponds with the Benton/Three Mile cultural phase and represents the site's greatest period of use. With 109 burials, Eva II produced the most burials and material culture remains (Bissett, 2014). Eva III (stratum I) includes the latest occupation, which represents the Big Sandy cultural phase, as well as the plow zone (Lewis and Lewis, 1961; Magennis, 1977). For this research, Strata III, IV, and V were excluded to maintain temporal contemporaneity with the other two sites.

The Cherry site (40BN74) is a Late Archaic site that is geographically and temporally comparable to Eva, located in Benton County, Tennessee, just east of the Big Sandy River and north of its junction with the Tennessee River. It was excavated in 1941, also sponsored by the TVA (Magennis, 1977). Cherry was assigned to the Big Sandy phase that corresponds with Eva's Stratum I by Lewis and Kneberg (1958); subsequent radiocarbon dating shows that its dates are instead contemporaneous with Eva's Three Mile Stratum II (Bissett, 2014). Unlike Eva, however, it represents only one occupation (approx. 7500-6300 cal BP)—no dates were obtained from a possible later occupation—and has a number of middens and pits. Remains were recovered from burials in the eastern portion of the site (Magennis, 1977; Auerbach, 2007). Sixteen total individuals (10 males, 6 females) from this site were examined.

The Ledbetter Landing site (40BN25) is also located in Benton County, Tennessee between Morgan's Creek and the Tennessee River (Lewis and Kneberg, 1947). It represents two occupations; relevant to this study is the first occupation, which dates to the Late Archaic, approximately 4500-4300 cal BP (Auerbach, 2007; Lewis and Kneberg, 1959; Bissett, 2014). 15 individuals (9 males, 6 females) from this site were examined.

The Archaic peoples who occupied Eva were sedentary foragers; material evidence from the Three Mile phase indicates that they relied heavily on freshwater sources (compared to terrestrial game animals). Ledbetter Landing likewise contained a multitude of riverine artifact assemblages. Eva and Ledbetter were both located close to waterways, and it is clear that the Archaic peoples who used these sites utilized freshwater resources. Cherry, on the other hand, was not immediately near a waterway and shows a dearth of evidence of freshwater exploitation. It has been suggested that the variance in types of artifacts represented in each site's assemblage indicates differential site function (Magennis, 1977). Furthermore, the stone tool assemblages of these sites indicate significant lithic use. Chipped stone characterized nearly half of the artifact assemblage at Eva, which also groundstone artifacts and bone and antler as well. The material culture at Cherry and Ledbetter were sparser, but similar artifacts were found (Bissett, 2014).

Limitations

As with any osteological study, there were certain limitations inherent in this research. The archaeological record by nature presents only a partial representation of any given population (Wood et al., 1992). Graves can only reflect those individuals who were buried. Although evidence suggests that these forager populations were not nomadic over a large geographic range, theories that these sites were periodically occupied indicate that remains from

large cemeteries like the ones studied here may represent only a brief cross-section in the population's history (Bissett, 2014).

Furthermore, these remains are several thousand years old; time, taphonomy, excavation, and curation takes its toll (Behrensmeyer, 1978; Trueman and Martill, 2002). As a result, the remains were limited in quantity and several elements were incomplete. Because only paired elements could be used for this type of analysis, the sample was further narrowed. Fortunately, the types of bones used in this study tend to preserve well—tubular bones are thicker and have less of the delicate, easily-damaged trabecular bone. Most of the radii were too fragmentary to use, but the majority of metacarpals were extremely well-preserved. Nevertheless, several elements were incomplete and had to be estimated. Estimation was only used for elements that were at least 60% complete; this ensured that the midshaft and either the proximal or distal articular surface was intact. Total length was then estimated based on the total length of the corresponding element on the opposite side. The midshaft was found based on the estimated total length, and then dorsopalmar and mediolateral breadths were taken and the midshaft cross-section was cast. It is worthy to note that this method of estimation assumed that the total length of paired elements were comparable; the relative incompleteness of one element was determined in relation to its complement from the opposite side. Approximately 12.8% of the sample required estimation.

ANALYTICAL METHODS

This section outlines the methodology used to obtain measurements, calculate biomechanical properties, and conduct statistical analyses.

Data Collection

Data from the bones were collected in two ways: external dimensions were measured manually, and casts of each bone were taken at midshaft. Total lengths of each metacarpal were measured to the nearest hundredth millimeter on a mini-osteometric board. The styloid process of the third metacarpal was excluded from the length measurement, as it does not contribute to the bone's biomechanical length. Radius total lengths were measured to the nearest millimeter on a portable PaleoTech Concepts osteometric board. Mitutoyo digital sliding calipers were used to measure diaphyseal breadths to the nearest hundredth of a millimeter; these measurements were recorded on a laptop via a direct input cord connected to the calipers. The midshaft mediolateral and dorsopalmar breadths of the radii and metacarpals were recorded. Intraobserver error was evaluated following the method outlined by White (2000). Differences from the mean measurement were expressed as a percentage; for most dimensions, the average measurement error was less than 1%. Data were recorded and calculations were made using Microsoft Excel 2013.

% Measurement Error ¹					
Measurement ²	Element ³				
	MC2 (L/R)	MC3 (L/R)	MC4 (L/R)	MC5 (L/R)	RAD (L/R)
Total length	0.07 / 0.02	0.07 / 0.03	0.02 / 0.03	0.03 / 0.07	0.13 / 0.09
DP breadth at midshaft	0.71 / 0.15	0.17 / 0.16	0.17 / 0.22	0.19 / 0.24	0.12 / 0.16
ML breadth at midshaft	0.62 / 0.24	0.29 / 0.24	0.22 / 0.29	0.2 / 0.25	0.1 / 0.16

¹ Error calculated according to White (2000); reported to the nearest 0.01%

² Length measured to the nearest mm, diaphyseal dimensions to the nearest hundredth mm; Planes are abbreviated: DP, dorsopalmar (anteroposterior for radii); ML, mediolateral

³ Elements are abbreviated: MC, metacarpal; RAD, radius; L, left; R, right

Additionally, external casts were made at the midshaft of each bone using Coltène/Whaledent President putty. The neutral axes were marked along the dorsal and lateral surfaces of each metacarpal shaft to properly line up the cast. Dorsopalmar and mediolateral breadths were taken at 30% and 70% along the metacarpal shafts, from which midpoints were determined; these were then used to triangulate the approximate neutral axis of the diaphysis in each plane. Using these to orient the bone, the metacarpals were set into an anatomical orientation. The President putty was applied in a slim ring along the midshaft circumference of each bone. The resulting cast produced an accurate representation of the midshaft cross-section. These casts were traced and scanned to Photoshop to prepare them for analysis. Each cross-sectional image was oriented in anatomical position, with the DP axis (AP for radii) vertical and ML axis horizontal. The cross-section itself was manually filled with black pixels; the medullary cavity was not considered in these analyses. These manipulated images were analyzed with a MATLAB code (provided by Dr. Benjamin Auerbach) to calculate the bone's cross-sectional properties. All data were determined from external dimensions; recent studies show, absent pathologies that decrease endosteal bone mass, that external dimensions alone provide reliable estimations of bone strength (Macintosh et al., 2013; Stock and Shaw, 2007; O'Neill and Ruff, 2004).

From the cross-sections, MATLAB generated several biomechanical measurements to be used in the analysis of directional asymmetry. Relevant to this study were measures of total area (TA), second moments of area for the dorsopalmar (I_{dp}) and mediolateral (I_{ml}) axes, the polar second moment of area (J), and maximum and minimum second moments of area (I_{max} , I_{min}). Measurements of asymmetry were converted to percent directional asymmetry (%DA) and percent absolute asymmetry (%AA):

$$\%DA = (\text{right-left}) / [(\text{right} + \text{left})/2] \times 100$$

$$\%AA = (\text{maximum-minimum}) / [(\text{maximum} + \text{minimum})/2] \times 100$$

Converting measures of asymmetry to percentages allows data from elements from different sexes and populations to be directly compared without standardizing by body mass, because the percent asymmetry of a given dimension is standardized by the size of that dimension. %DA reflects directionality and magnitude of asymmetry in a given dimension, signaling right-biased asymmetry with positive values and left-biased asymmetry with negative values. %AA reflects total asymmetry present in a given dimension, regardless of directionality (Auerbach and Ruff, 2006).

The ratios of second moments of area about the dorsopalmar (DP) and mediolateral (ML) planes, I_{dp}/I_{ml} , and the ratio of maximum and minimum second moments of area, I_{max}/I_{min} , were likewise used to circumvent the need for size standardization (Ruff and Hayes, 1983). More importantly, however, these ratios represent indices of cross-sectional shape. I_{dp}/I_{ml} measures the bending strength in the dorsopalmar plane relative to the mediolateral plane. Ratios approaching 1 indicate even distribution of bone about these axes (a more circular cross-section); ratios larger than 1 indicate bone is distributed more along the dorsopalmar plane, whereas ratios less than 1 reflect strengthening along the mediolateral plane. I_{max} and I_{min} are always perpendicular to each other and measure the relative maximum bending strength of the bone. The ratio I_{max}/I_{min} follows the same logic as that of I_{dp}/I_{ml} , except the ratio will always be greater than or equal to 1.

Statistical Methods

Nonparametric statistics were used to examine these data according to the precedent set by Auerbach and Ruff (2006), which established the preference for using nonparametric tests with percentage data due to non-normal distributions. Moreover, the overall sample in this study was relatively small, and considering that several tests required further subdivisions of the data (i.e. by sex, by metacarpal), the data did not conform to the rules of normality. Thus parametric statistics were inappropriate for this research. All statistical analyses were conducted using IBM SPSS 20.

For all analyses, data from the sites were pooled. Mann-Whitney *U*-tests (the nonparametric equivalent of a two-sample *t*-test) were used to evaluate sex-based differences in percentage data (% DA and %AA) and to compare these data for each dimension between elements (i.e. %DA of TA between MC2 and MC5). Kruskal Wallis tests (the nonparametric equivalent of ANOVA) evaluated these data for differences in each dimension among elements (i.e. %DA of TA among MC2, MC3, MC4, and MC5). Because several analyses were used, the critical alpha for statistical significance was set conservatively at $p < 0.01$, rather than the standard $p < 0.05$. A conservative alpha level was chosen to limit Type I error, the likelihood of which increases as the number of comparisons increases. Both significant and non-significant results were examined for trends to determine patterns of asymmetry across groups. The following chapter presents the results of these analyses.

CHAPTER 3: RESULTS

This chapter describes the results of the statistical analyses outlined in Chapter 2. All interpretations of these data will be reserved for the following chapter, Discussions and Conclusions.

Statistical Analyses of Sex Differences

Medians and means of percent directional asymmetry and percent absolute asymmetry for each element by site and by sex are presented in the Appendix. For all analyses, the sites were pooled based on the overall comparability of the measurements of asymmetry among sites shown by the descriptive statistics.

The cross-sectional properties of each element were compared between the sexes using Mann-Whitney *U*-tests to evaluate differences. Results are presented in Tables 3.1 and 3.2, and boxplots of non-significant trends are found in Figure 3.1. As mentioned in Chapter 1, previous studies have established that males tend to demonstrate more asymmetry than females, which is especially pronounced in forager populations. All elements were analyzed, and while none showed statistical significance ($p < 0.01$), the second metacarpal was the only element that showed a trend of difference between the sexes. For MC2, females showed more right-biased directional asymmetry and greater absolute asymmetry in several dimensions than males.

Table 3.1. *p*-values for %DA of Males v. Females

Cross-sectional dimension	MC2 <i>p</i>value	MC3 <i>p</i>value	MC4 <i>p</i>value	MC5 <i>p</i>value	RAD <i>p</i>value
TA	0.05	0.963	0.383	0.911	0.226
I_{dp}/I_{ml}	0.613	0.982	0.557	0.231	0.450
I_{max}/I_{min}	0.468	0.799	0.578	0.736	0.821
I_{dp}	0.073	0.781	0.458	0.501	0.070
I_{ml}	0.03	0.908	0.516	0.575	0.496
I_{max}	0.078	0.908	0.477	1.00	0.545
I_{min}	0.032	0.799	0.557	0.956	0.082
J	0.032	1.00	0.421	0.985	0.131

* Asterisks indicate significant differences ($p < 0.01$) between males and females

Table 3.2. *p*-values for %AA of Males v. Females

Cross-sectional dimension	MC2 <i>p</i>value	MC3 <i>p</i>value	MC4 <i>p</i>value	MC5 <i>p</i>value	RAD <i>p</i>value
TA	0.015	0.319	0.781	0.432	0.496
I_{dp}/I_{ml}	0.223	0.677	0.902	0.525	0.940
I_{max}/I_{min}	0.538	0.660	0.853	0.852	0.597
I_{dp}	0.042	0.889	0.557	0.025	0.545
I_{ml}	0.014	0.082	0.829	0.681	0.406
I_{max}	0.036	0.889	0.516	0.155	0.762
I_{min}	0.044	0.110	0.643	0.970	0.705
J	0.044	0.562	0.805	0.432	0.226

* Asterisks indicate significant differences ($p < 0.01$) between males and females

Figure 3.1 contains boxplots of the trends present between the sexes in the cross-sectional properties of the second metacarpal. The graphs give a general outline of the discernible patterns of asymmetry; it is clear that females demonstrate more (though not significantly more) right bias and absolute asymmetry than males. Relevant cross-sectional properties for comparisons of

directional asymmetry (due to relatively small p -values) include total area (TA), the second moments of area I_{ml} and I_{min} , and the polar second moment of area (J).

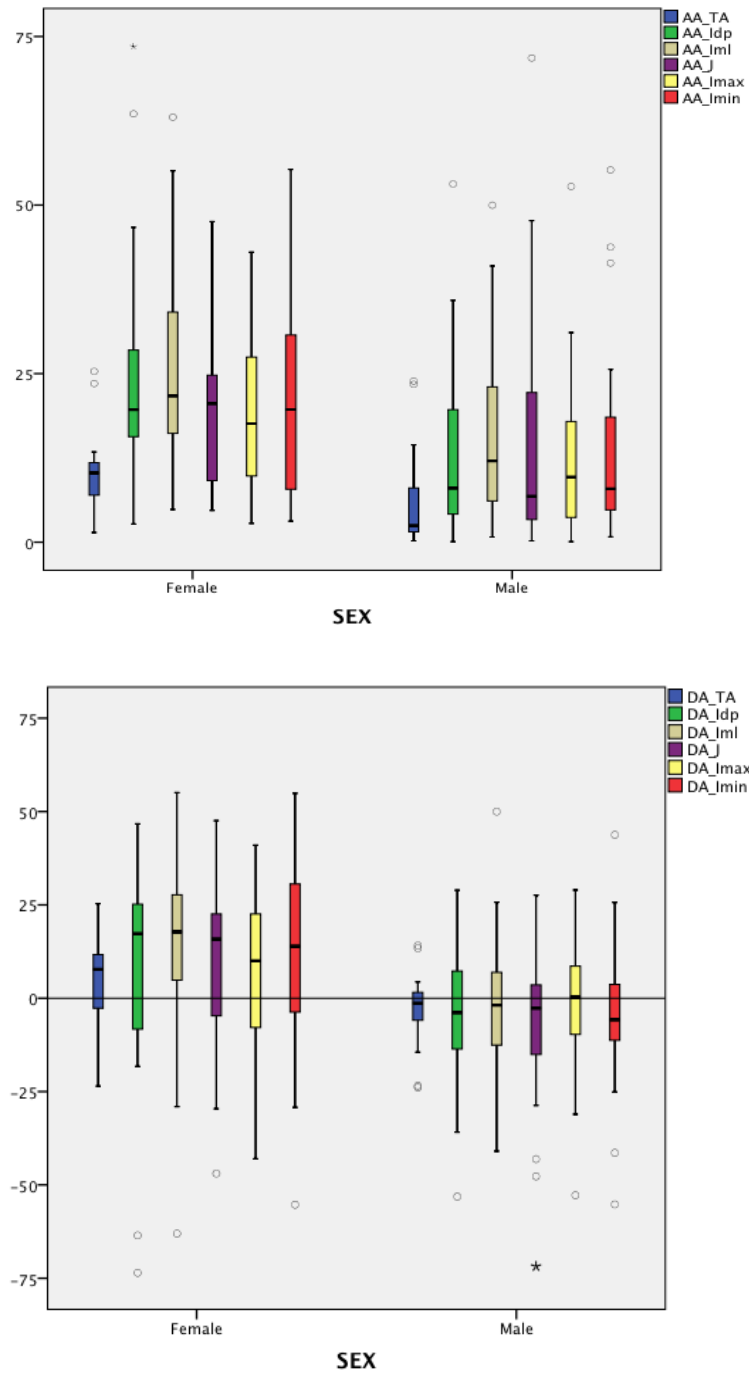


Figure 3.1. Comparison of %AA and %DA in MC2 between Males and Females

Statistical Analyses among Elements within the Same Sex

The trends produced by the previous statistical analyses established that, though not significant, there was enough difference between males and females to preclude their being pooled for further analyses. Thus the sample was subdivided by sex to conduct Kruskal Wallis tests to compare cross-sectional properties among elements. Results of analyses among the metacarpals are presented in Tables 3.3 and 3.4. Boxplots of significant differences and non-significant trends appear in Figures 3.2, 3.3, and 3.4. Comparisons among elements were not significantly different for females; males, however, produced significant values for a number of dimensions.

Table 3.3
***p*-values of %DA among Metacarpals 2-5**

Cross-sectional dimension	Males <i>p</i> value	Females <i>p</i> value
TA	0.009*	0.237
I_{dp}/I_{ml}	0.023	0.753
I_{max}/I_{min}	0.138	0.449
I_{dp}	0.155	0.472
I_{ml}	0.004*	0.320
I_{max}	0.163	0.441
I_{min}	0.015	0.261
J	0.01*	0.287

*Asterisks indicate significant differences ($p < 0.01$).

Table 3.4
***p*-values of %AA among Metacarpals 2-5**

Cross-sectional dimension	Males <i>p</i> value	Females <i>p</i> value
TA	0.009*	0.345
I_{dp}/I_{ml}	0.063	0.401
I_{max}/I_{min}	0.401	0.359
I_{dp}	0.023	0.069
I_{ml}	0.064	0.712
I_{max}	0.009*	0.488
I_{min}	0.008*	0.266
J	0.026	0.447

*Asterisks indicate significant differences
($p < 0.01$).

A second set of Kruskal Wallis tests compared cross-sectional properties among the metacarpals and the radius. Analysis of properties in the female sample were not significant, but for males the values that were reported above (Tables 3.3 and 3.4) as significant remained so. The boxplots below and in Figure 3.4 (which depicts dimensions with significant and extremely low, but not significant *p*-values) show that the radius appears to have similar directional asymmetry to the metacarpals in all but total area, second moment of area of the x-axis (I_{ml}) and the polar second moment of area.

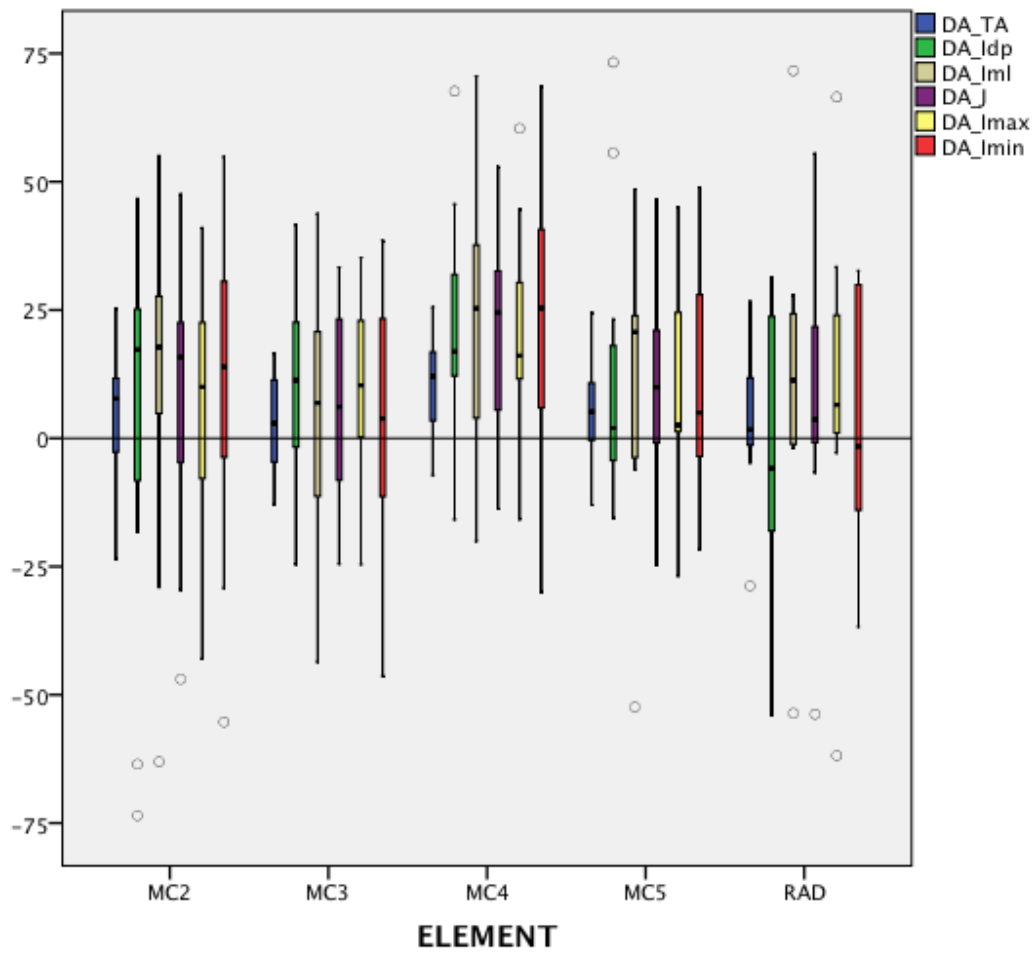


Figure 3.2. % Directional Asymmetry of Females Compared among Elements

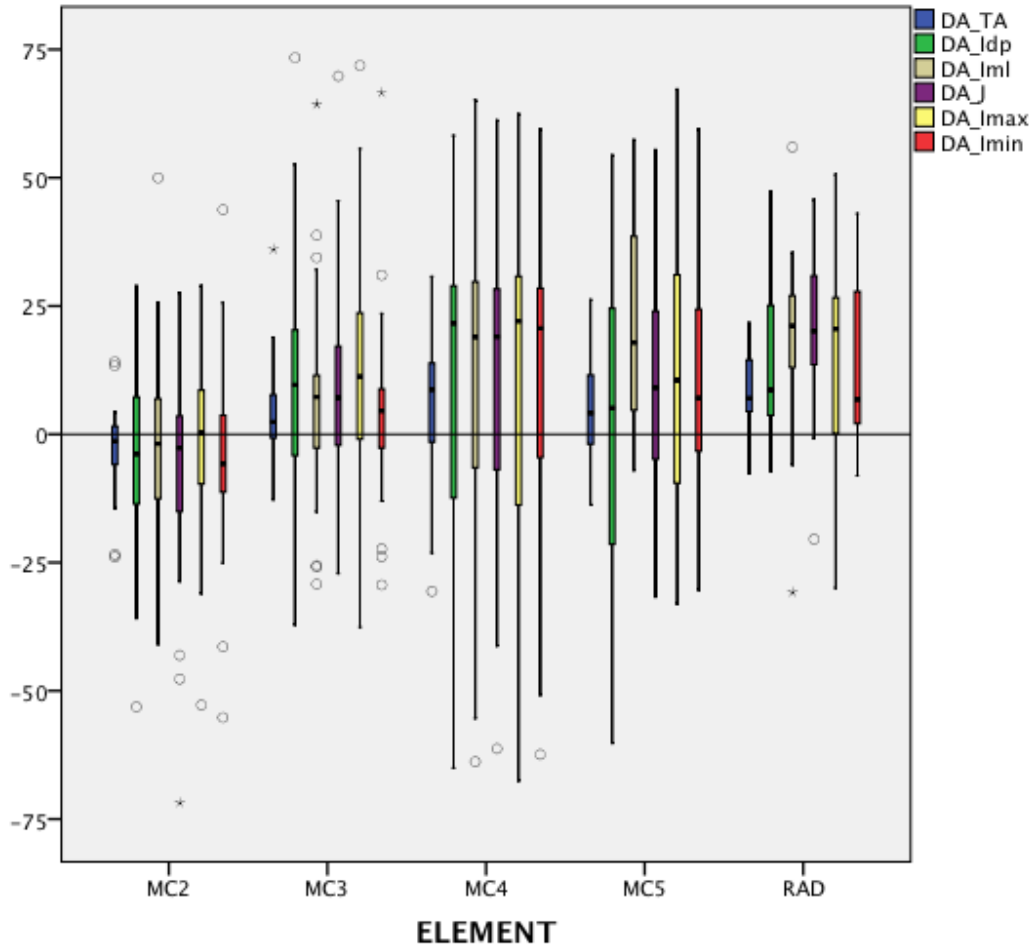


Figure 3.3. % Directional Asymmetry of Males Compared among Elements

The patterns that appear in the boxplots in Figures 3.2 and 3.3 show several trends that are further investigated in the following section “Comparisons between Two Elements.” Figure 3.3 shows it best, since there are actual significant differences represented, but the differences among female elements shown in Figure 3.2 also supports certain trends (though to a lesser extent). The second and fourth metacarpals tend to show the most disparate values. For most dimensions, the second metacarpal appears to show the least amount of absolute asymmetry and even left-biased directional asymmetry, while the fourth metacarpal demonstrates the most absolute asymmetry and the most right-biased asymmetry. The third and the fifth metacarpal are

largely comparable, however, the fifth metacarpal does demonstrate some anomalies which will be explored further in next section.

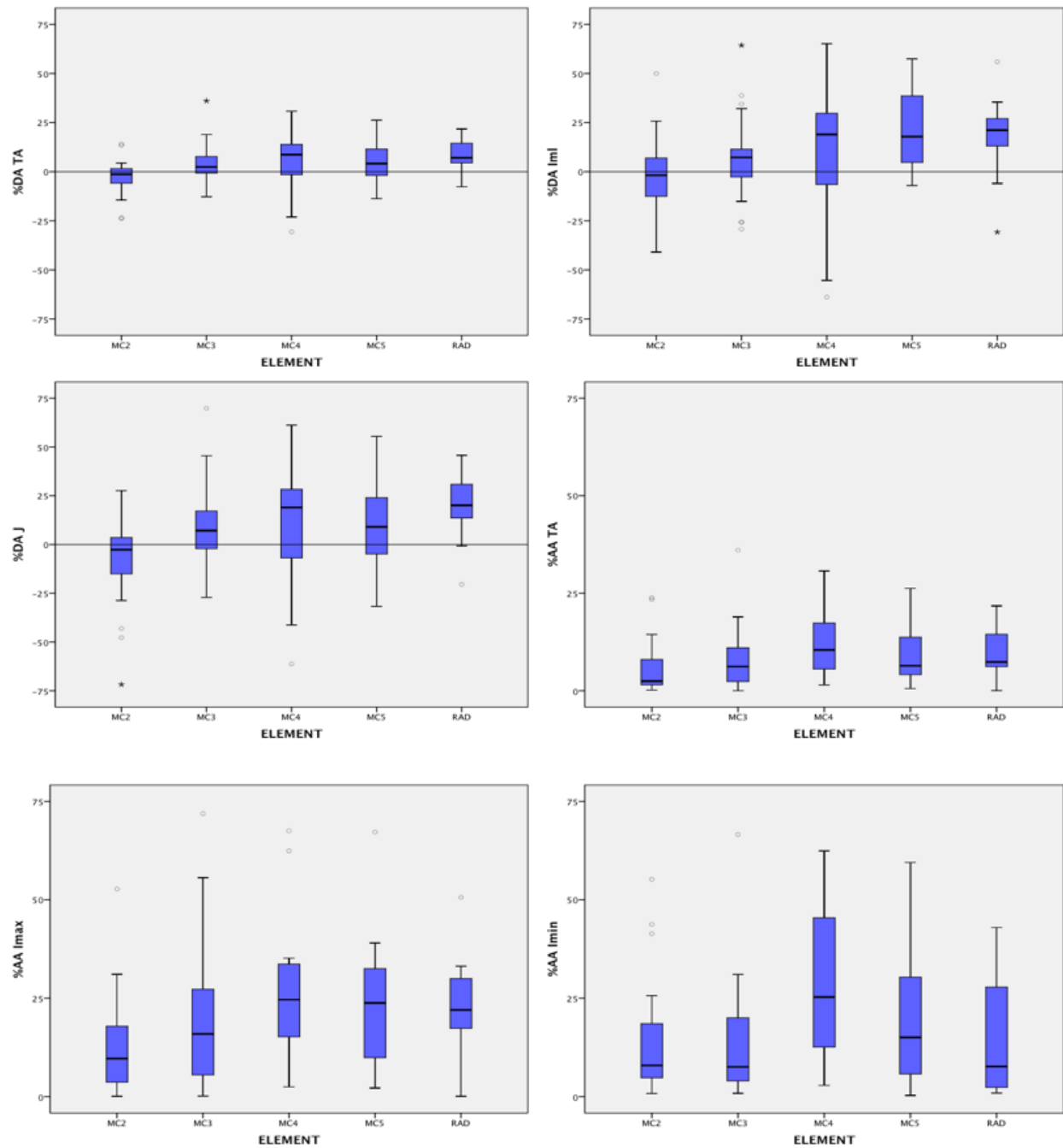


Figure 3.4. Boxplots of %AA and %DA Comparisons between Elements

Comparisons between Two Elements

Based on the boxplots of the data, the comparisons of most interest were the second and fourth metacarpal, the second and fifth metacarpal, and the second metacarpal and the radius. Mann-Whitney *U*-tests were used to evaluate the differences in cross-sectional properties between these elements. Again, the data were separated based on sex. Females did not show statistical significance in any of these comparisons.

Comparisons between the second and fourth metacarpals in the male sample yielded several significant values; these data are reported in Table 3.5. Figures 3.5 and 3.6 contain boxplots of these comparisons. Particularly of interest are the differences in total area and polar second moment of area, with values of $p < 0.01$. The boxplots show that the fourth metacarpal appears to demonstrate more right-biased asymmetry and a greater magnitude of asymmetry than the second metacarpal for all graphically depicted values.

Table 3.5
***p*-values of %DA and %AA of Male MC2 v MC4**

Cross-sectional dimension	%DA p-value	%AA p-value
TA	0.005*	0.003*
I_{dp}/I_{m1}	0.482	0.188
I_{max}/I_{min}	0.220	0.153
I_{dp}	0.033	0.018
I_{m1}	0.018	0.019
I_{max}	0.041	0.001*
I_{min}	0.006*	0.004*
J	0.005*	0.006*

*Asterisks indicate significant differences ($p < 0.01$).

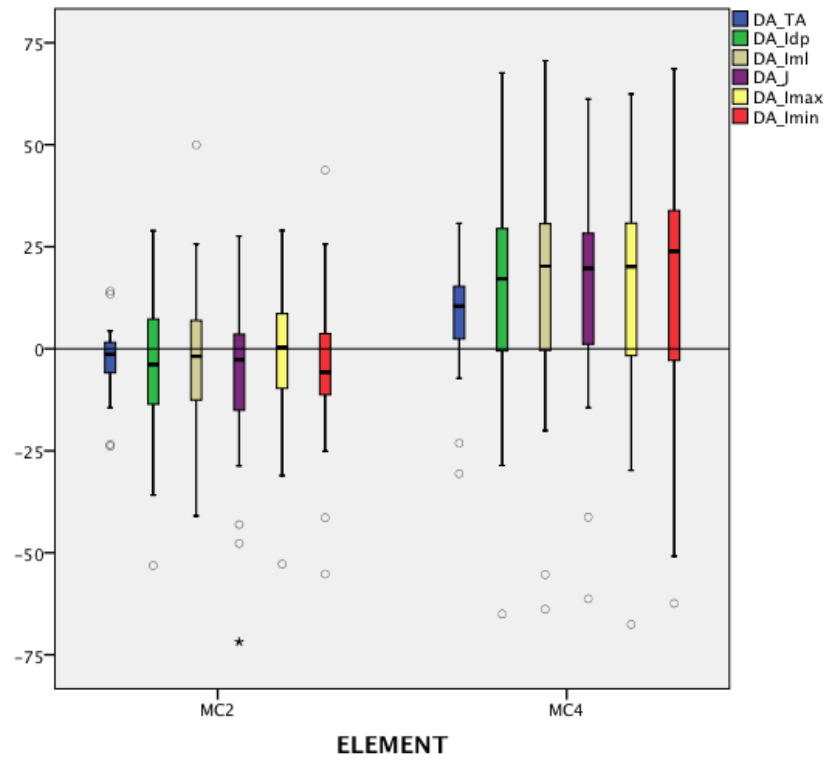


Figure 3.5. % Directional Asymmetry Compared between Male MC2 and MC4

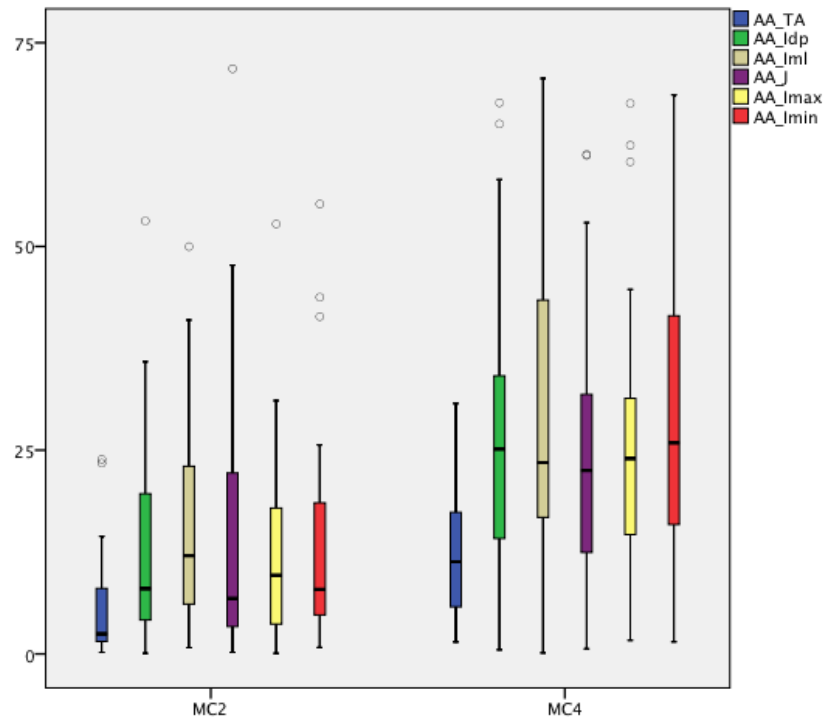


Figure 3.6. % Absolute Asymmetry Compared between Male MC2 and MC4

Further analyses were carried out to compare the second and fifth metacarpal. Results are reported in Table 3.6. Again, only males produced statistical significance. Furthermore, only one comparison reached statistical significance—that of the percent directional asymmetry of I_{ml} — but very small p -values are also seen for total area, the ratio I_{dp}/I_{ml} , and the polar second moment of area. Comparisons of percent absolute asymmetry did not produce statistically significant values, though graphical comparisons show that the fifth metacarpal appears to have a greater magnitude of asymmetry than the second metacarpal. Boxplots of significant differences and non-significant trends can be found in Figures 3.7 and 3.8.

Table 3.6
 p -values for %DA and %AA of Male MC2 v. MC5

Cross-sectional dimension	%DA p-value	%AA p-value
TA	0.013	0.023
I_{dp}/I_{ml}	0.014	0.016
I_{max}/I_{min}	0.842	0.991
I_{dp}	0.581	0.012
I_{ml}	0.001*	0.366
I_{max}	0.136	0.018
I_{min}	0.023	0.353
J	0.016	0.018

*Asterisks indicate significant differences
($p < 0.01$).

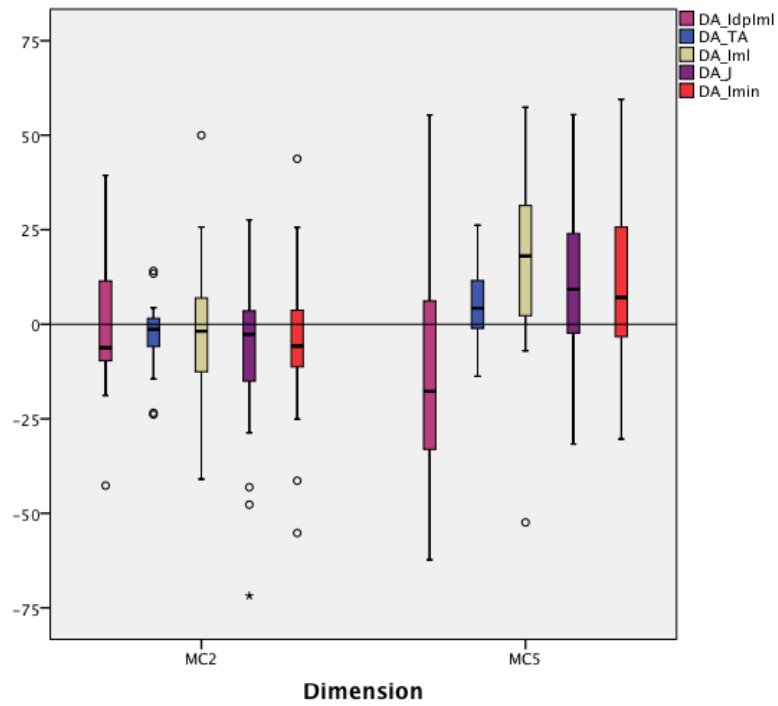


Figure 3.7. % Directional Asymmetry Compared between Male MC2 and MC5

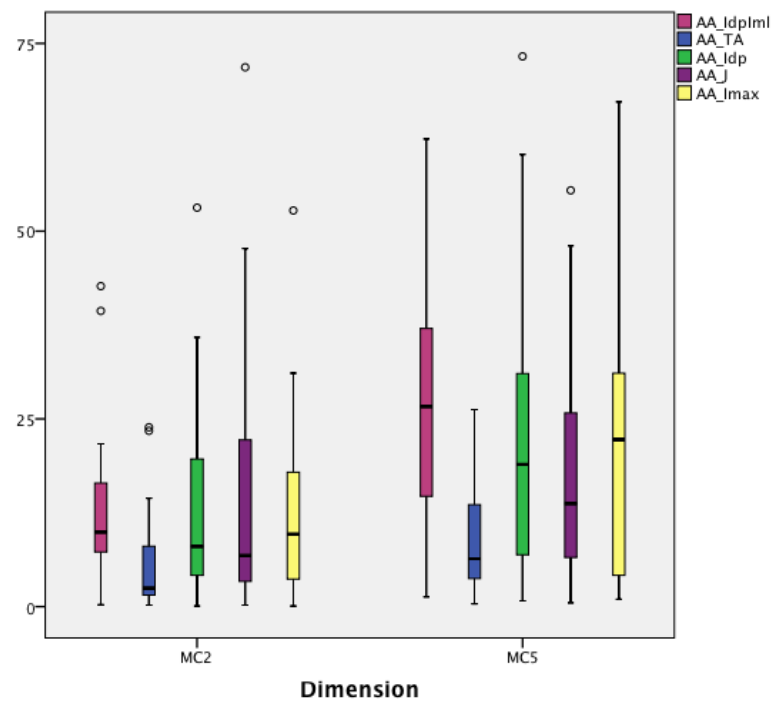


Figure 3.8. % Absolute Asymmetry Compared between Male MC2 and MC5

The final comparison was made between the second metacarpal and the radius. Results are reported in Table 3.7. Only comparisons among males produced significant differences. Percent directional asymmetry of total area, the second moment of area I_{ml} , and polar second moment of area were the only p -values that were statistically significant. Comparisons of percent absolute asymmetry, however, did not yield significant p -values. This would suggest that the amount of asymmetry between the second metacarpal and the radius is not different; only the direction of asymmetry. Figure 3.9 shows boxplots of significant differences and non-significant trends present in the comparisons of directional asymmetry.

Table 3.7
 p -values of %DA and %AA of Male MC2 v. Radius

Cross-sectional dimension	%DA p-value	%AA p-value
TA	0.004*	0.137
I_{dp}/I_{ml}	0.158	0.214
I_{max}/I_{min}	0.495	0.789
I_{dp}	0.137	0.436
I_{ml}	0.006*	0.103
I_{max}	0.014	0.098
I_{min}	0.103	0.661
J	0.004*	0.165

*Asterisks indicate significant differences
($p < 0.01$).

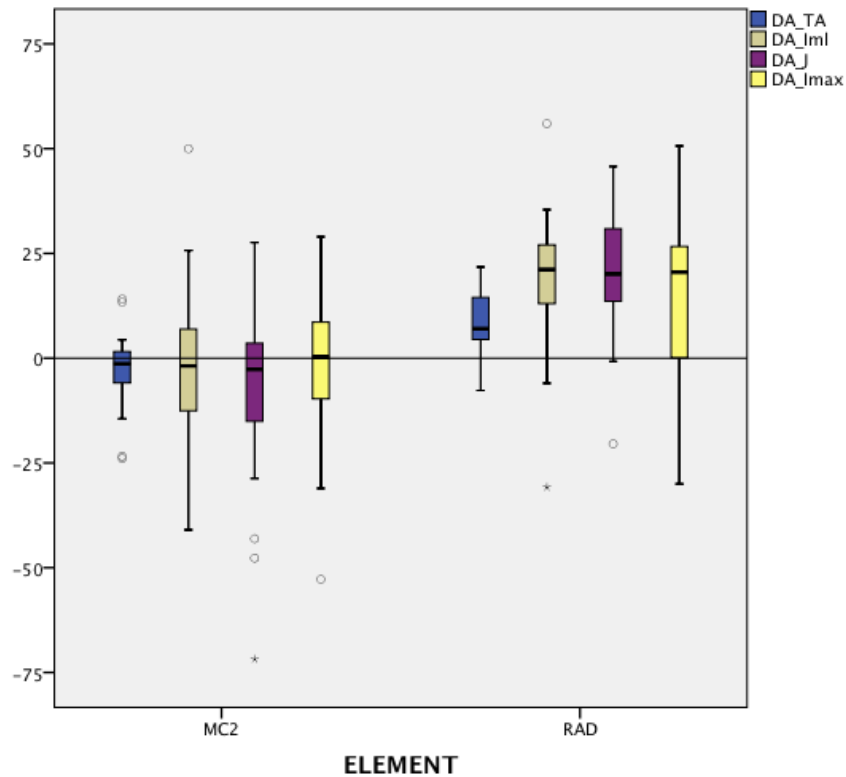


Figure 3.9. % Directional Asymmetry Compared between Male MC2 and Radius

Overall, the male second metacarpal appears to present the primary anomaly. The second metacarpal is the only bone to show sex-based differences, and as the graphical depictions of comparisons among elements show, it is the only bone to consistently show little absolute asymmetry, small values of right-biased asymmetry, and even left-biased asymmetry.

The indices of cross-sectional shape (I_{dp}/I_{ml} and I_{max}/I_{min}) were largely excluded from the graphical representations. Despite the evidence based on previous research, they did not yield statistically significant values for any of the analyses. It was expected that not only would these measures be significant, but that they would reliably reflect asymmetry. Instead, comparisons of total area (TA) and the polar second moment of area (J) consistently produced either significant

or very low p -values. As mentioned previously, all of these data will be interpreted in the following chapter, “Discussion and Conclusions.”

CHAPTER 4: DISCUSSION AND CONCLUSIONS

The purpose of this study was to examine the cross-sectional diaphyseal geometry of metacarpals to evaluate patterns of directional asymmetry across the palmar arch within a physically active set of human populations. While laterality has been the focus of scientific inquiry across a number of disciplines, including anthropology, this research is unique in its consideration of the cross-sectional properties of the entire digital ray. Consequently, the results of this study have implications for future research using metacarpals; previously, researchers have assumed that the properties of the second metacarpal accurately represent those of the entire digital ray. The results of this study depart from this supposition, arguing instead for individualized attention to the properties of each metacarpal. Accordingly, this study also impacts research into handedness based on the metacarpals.

The following chapter examines the results of the statistical analyses set forth in Chapter 3 and considers their consequences for the hypotheses presented in Chapter 1. Based on previous research (see Introduction), it was posited that the sample of Archaic individuals examined here would demonstrate right-biased asymmetry, and likely this asymmetry would present more strongly in males. It was also generally expected that the dominant limb would exhibit a rounder diaphyseal cross-section. Of course, there were several limitations to this study, which were outlined in Chapter 2 and are relevant to the interpretation of the statistical analyses presented in the previous chapter. The small sample size, in particular, cautions against overstating the impact and applicability of the results and implications discussed here.

The major findings of this study challenged the hypotheses recapitulated above. Results indicated that sexual dimorphism was far from systemic; instead, there were no statistically

significant differences between males and females. However, analysis of the trends of asymmetry indicates that the second metacarpal clearly demonstrates more absolute asymmetry and more right-biased directional asymmetry in females compared to males. It was also assumed that the diaphyseal cross-sections of the metacarpals of the dominant limb would demonstrate more circularity. On the contrary, results showed that the ratios of cross-sectional shape (I_{dp}/I_{ml} and I_{max}/I_{min}) were not significantly asymmetric in any of the statistical analyses presented in Chapter 3, and therefore were not useful here in examining handedness. Instead, total area (TA) and the polar second moment of area (J) consistently demonstrated statistical significance. This indicates that while the cross-sections of the metacarpals of the dominant limb do not necessarily demonstrate more circularity, they were subject to greater axial and torsional stresses and are likewise strengthened to withstand those stresses. Finally, the overall pattern that emerged from the results of the statistical analyses indicates that absolute and directional asymmetry increase medially across the digital ray and, as predicted, the directional asymmetry present in this sample was overwhelmingly right-biased.

Sexual Dimorphism of Directional Asymmetry

Contrary to previous research, sexual dimorphism was not statistically significant in this sample. Except the second metacarpal, the percent asymmetry of the cross-sectional properties of the metacarpals were comparable between males and females. Even considering the dimorphic MC2, the overall pattern of directional asymmetry persisted: the second and third metacarpals demonstrated considerably less absolute asymmetry and less right-biased asymmetry than the more medial fourth and fifth metacarpals (the significance of this pattern will be discussed in the following section).

It is worthy of note, however, that this pattern of asymmetry is more pronounced in the male sample; indeed, the results presented in Chapter 3 indicate that statistical significance only emerged in the male sample. Trends in the data show that females tended to have slightly more absolute and directional asymmetry than males in general, which could be used to argue that females engaged in more unimanual tasks than did males, resulting in cross-sections that showed greater strength properties in their dominant limb. Moreover, these unimanual tasks almost certainly required a power grip, thereby recruiting the palm and subjecting the metacarpals to strain (Marzke and Shackley, 1987).

Males may have participated in more bimanual tasks, but the patterns in this sample could also be the result of using a precision grip more frequently than a power grip, which would impact the strength properties reflected in the metacarpals. Prehistoric tool manufacture has been shown through experimental archaeology to rely more heavily on a precision grip rather than a power grip, which results in more detailed, delicate stone tools (Marzke and Shackley, 1987; Marzke, 1997). Though material culture was sparse at the Cherry and Ledbetter Landing sites (see Chapter 2), Eva yielded a number of stone artifacts: chipped stone represented nearly half of the total site assemblage at Eva, and a number of groundstone artifacts were found as well (Bissett, 2014). Of course, the archaeological record reflects only those materials that preserve well over time; consequently, the assemblage is more biased toward more durable materials rather than perishable materials, which may skew the interpretation of male and female activities. However, if males were predominantly engaged in tool manufacturing (as the material culture would suggest), it follows that asymmetry would be more difficult to ascertain using the metacarpals, as these elements are not directly engaged in the precision grip necessary for flint knapping. Though they showed less absolute and directional asymmetry than females, males did

show more variation across the digital ray, yielding statistically significant results for comparisons across the palmar arch and between elements. These results will be discussed in the following section, “Comparisons among Elements.”

Material culture may also potentially explain the trends observed in females. As mentioned, females generally demonstrated more absolute and directional asymmetry than males. Because the metacarpals experience strain when the palm is recruited, it follows that females routinely engaged in activities that demanded a power grip in order to engender changes to the strength properties of the metacarpals. Moreover, these activities were likely unimanual, reflected in the resulting directional asymmetry. Groundstone functional classes associated with food processing (such as pestles) were found at the archaeological sites represented by the sample (Bissett, 2014). If women routinely engaged in this type food processing, it could have produced the asymmetry reflected in the results. This activity would be unimanual and it requires a power grip; both of these would impact the strength properties of the metacarpals and result in greater directional asymmetry, consistent with the results of this study.

As mentioned, the second metacarpal is the only element that showed clear differences (though not statistically significant differences) between males and females. The metacarpals gain more freedom of movement medially; the second and third metacarpals are the most stable in the hand (see Introduction). Compounded with the apparent lack of routine unimanual tasks that require power grip among males, the low level of asymmetry found in the second metacarpal of males may be a combination of the relative stability of the second metacarpal and the overall lack of strains that would directly impact its strength properties. Marzke and Shackley (1987) also indicate that stone tool manufacturers frequently stabilize the stone against the second metacarpal, gripping it with the thumb and forefinger, thereby ensuring the second metacarpal is

a passive element during tool manufacture. Though the cause of this departure from expected results is unknown, it does illustrate the errors of using the cross-sectional properties of the second metacarpal as an accurate representation of those of the entire digital array.

Comparisons among Elements

Kruskal-Wallis tests comparing the cross-sectional properties across the digital ray only yielded statistically significant values within the male sample, although trends in both males and females show that both absolute and directional asymmetry increase medially, with greater degrees of both measurements in the fourth and fifth metacarpals. Contrary to the hypothesis, however, the indices of cross-sectional shape were not, in most cases, significantly impacted by handedness. Instead, the most consistently significant properties were total area (TA) and polar second moment of area (J).

The general increase in the magnitude of asymmetry and right-biased asymmetry of the medial metacarpals likely reflects the greater freedom of movement they experience compared to the second and third metacarpals. Specific to males, though, results indicate that the total area and polar second moments of area increase significantly. This suggests that the medial palm is subject to greater compressive and torsional strains than the lateral palm, the greatest difference between the second metacarpal and the fourth metacarpal. To recapitulate, although males have less asymmetry compared to females, the strength properties of their metacarpals vary more than those of females. However, it should be noted that these differences between elements in males stem from the second metacarpal; due to its very low asymmetry, comparisons between MC2 and other metacarpals produce statistical significance. Therefore, males do not necessarily experience greater overall compressive and torsional strains in their medial palms than do

females, but rather males experience less overall compressive and torsional strains in their lateral palms than do females. Again, a reasonable explanation is that one of the primary manual tasks males engage in—tool manufacturing—demands the passive recruitment of MC2 as a stabilizing factor, thus it is not mechanically engaged in this activity.

This is the first study to examine laterality across the entire digital ray, and one of the first to evaluate handedness based on the diaphyseal cross-sectional properties of the metacarpals. Here, nonparametric statistics were used to analyze a relatively small sample. While the trends produced can reliably indicate patterns for this population, this study has neither enough data nor enough statistical power to draw absolute conclusions from the results. The results of this study produced unexpected patterns of directional asymmetry. To more fully understand these patterns that have emerged across the palmar arch, further research is essential to generate more data and determine if the patterns observed in this research represent systemic laterality across populations or are unique to populations in western central Tennessee. Consequently, a larger sample size and a wider geographic distribution would be necessary.

CONCLUSIONS

In sum, this study represents an initial investigation into the asymmetry of the digital ray of the Archaic foragers of Tennessee using the diaphyseal cross-sectional properties of metacarpals. The goal was to determine if sexual dimorphism was present in these elements, and if patterns of directional and absolute asymmetry persisted across the palm. Contrary to the hypotheses, sexual dimorphism was present in only a single element, and females had more absolute and directional asymmetry within that element. Overall, however, males and females both demonstrated increasing absolute asymmetry and greater right-biased asymmetry in the

medial palm, which can be attributed to the greater freedom of movement possible in the medial metacarpals. Males showed statistically significant differences between the strength properties of the elements, which indicated that the medial hand was better able to withstand torsional and compressive forces. These differences are likely due to the same activities that caused the aberrant second metacarpal; rather than unusually more torsional and compressive stress in the medial hand, it is likely the lateral hand simply was not subject to a great deal of torsional and compressive stresses.

Overall, this study cautions against using a single metacarpal to represent the rest of the metacarpal bones' strength properties. Clearly, the cross-sectional properties have significant differences among the metacarpals that should be taken into account. More research is necessary, however, to better establish the patterns of asymmetry presented in this thesis and to begin to understand their causes.

REFERENCES

- Auerbach, B.M. (2007). Human skeletal variation in the New World during the Holocene: Effects of climate and subsistence across geography and time. Ph.D. diss, Center for Functional Anatomy & Evolution: Johns Hopkins University School of Medicine.
- Auerbach, B.M. & Ruff, C.B. (2006). Limb bone bilateral asymmetry: Variability and commonality among modern humans. *Journal of Human Evolution*, 50, 203-218.
- Behrensmeyer, A.K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology*, 4(2): 150-162.
- Bissett, T.G. (2014). The western Tennessee shell mound Archaic: Prehistoric occupation in the lower Tennessee River Valley between 9000 and 2500 cal yr BP. Ph.D. diss, University of Tennessee, Knoxville.
- Browman, D.L., Fritz, G.J., and Watson, P.J. (2013). Origins of food-producing economies in the Americas. In *The Human Past: World Prehistory and Development of Human Societies (3rd Edition)*. Chris Scarre (ed.). London: Thames and Hudson, Ltd.
- Bridges, P.S. (1989). Changes in activities with the shift to agriculture in the southeastern United States. *Current Anthropology*, 30 (3): 385-394.
- Bridges, P.S., Blitz, J.H., and Solano, M.C. (2000). Changes in long bone diaphyseal strength with horticultural intensification in west-central Illinois. *American Journal of Physical Anthropology*, 112: 217-238.
- Byrne, R.W. and Byrne, J.M. (1991). Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. berengei*). *Cortex*, 27 (4): 521-546.
- Case, D.T. and Ross, A.H. (2007). Sex determination from hand and foot bone lengths. *Journal*

- of Forensic Science*, 52 (2): 264-270.
- Churchill, S.E. and Formicola, V. (1997). A case of marked bilateral asymmetry in the upper limbs of an upper Palaeolithic male from Barma Grande (Liguria), Italy. *International Journal of Osteoarchaeology*, 7:18-38.
- Corballis, M.C. (2003). From mouth to hand: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences*, 26:199–260.
- Corballis, M.C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transactions of the Royal Society of Biological Sciences*, 364: 867–879.
- Cowin S.C., Hart R.T., Balser J.R., Kohn D.H. (1985). Functional adaptation in long bones: establishing in vivo values for surface remodeling rate coefficients. *Journal of Biomechanics*, 18:665–684.
- Currey, J.D. (2002). *Bones: Structure and Mechanics*. Princeton: Princeton University Press.
- Ferretti, J.L., Capozza, R.F., and Zancetta, J.R. (1996). Mechanical validation of a tomographic (pQCT) index for noninvasive estimation of rat femur bending strength. *Bone*, 18 (2): 97-10.
- Frost, G.T. (1980). Tool behavior and the origins of laterality. *Journal of Human Evolution*, 9: 447-459.
- Garn, S.M., Mayor, G.H., and Shaw, H.A. (1976). Paradoxical bilateral asymmetry in bone size and bone mass in the hand. *American Journal of Physical Anthropology*, 45: 209-210.
- Garn, S.M., Sullivan, T.V., and Decker, S.A. (1991). On the optimum number of metacarpals for roentgenogrammetric measurement. *American Journal of Physical Anthropology*, 85:229-232.

- Glencross, B. and Agarwal, S.C. (2010). An investigation of cortical bone loss and fracture patterns in the Neolithic community of Catalhoyuk, Turkey using metacarpal radiogrammetry. *Journal of Archaeological Science*, 38: 513-521.
- Herrmann, N.P. (2002). Biological affinities of Archaic period populations from west-central Kentucky and Tennessee. Ph.D. diss, University of Tennessee.
- Hopkins, W.D., Bard, K.A., Jones, A. and Bales, S.L. (1993). Chimpanzee hand preference in throwing and infant cradling: Implications for the origin of human handedness. *Current Anthropology*, 34 (5): 786-790.
- Jaworski, Z.F.G., Liskova-Kiar, M., and Uhthoff, H.K. (1980). Effect of long-term immobilization on the pattern of bone loss in older dogs. *Journal of Bone and Joint Surgery*, 62-B (1): 104-110.
- Jones H.H., Priest, J.D., Hayes, W.C., Tichenor, C.C. and Nagel, D.A. (1977). Humeral hypertrophy in response to exercise. *Journal of Bone and Joint Surgery*, 59:204-208.
- Lazenby, R.A. (1995). Non-circular geometry and radiogrammetry of the second metacarpal. *American Journal of Physical Anthropology*, 97:323-327.
- Lazenby, R.A. (1998a). Second metacarpal cross-sectional geometry: rehabilitating a circular argument. *American Journal of Human Biology*, 10:747-756.
- Lazenby, R.A. (1998b). Second metacarpal midshaft geometry in a historic cemetery sample. *American Journal of Physical Anthropology*, 106: 157-167.
- Lazenby, R.A. (2002a). Skeletal biology, functional asymmetry, and the origins of “handedness.” *Journal of Theoretical Biology*, 218: 129-138.
- Lazenby, R.A. (2002b). Population variation in second metacarpal sexual size dimorphism. *American Journal of Physical Anthropology*, 118: 378-384.

- Lazenby, R.A. (2002c). Skeletal biology, functional asymmetry, and the origins of “handedness.” *Journal of Theoretical Biology*, 218: 129-138.
- Lazenby, R.A. (2002d). Circumferential variation in human second metacarpal cortical thickness: Sex, age, and mechanical factors. *The Anatomical Record*, 267: 154-158.
- Lazenby, R.A., Cooper, D.M.L., Angus, S. & Hallgrímsson, B. (2008). Articular constraint, handedness, and directional asymmetry in the human second metacarpal. *Journal of Human Evolution*, 54: 875-885.
- Lewis, T.M.N. and Kneberg, M. (1947). *The Archaic Horizon in Western Tennessee*. In The University of Tennessee Record Extension Series, 23(4). Knoxville: The University of Tennessee Press.
- Lewis, T.M.N. and Kneberg, M. (1958). *Tribes That Slumber: Indians of the Tennessee Region*. Knoxville: The University of Tennessee Press.
- Lewis, T.M.N. and Kneberg, M. (1959). The archaic culture in the middle south. *American Antiquity*, 25(2): 161-183.
- Lewis, T.M.N. and Lewis, M.K. (1961). *Eva: An Archaic Site*. Knoxville: The University of Tennessee Press.
- Lieberman, D.E., Devlin, M.J., and Pearson, O.M. (2001). Articular area responses to mechanical loading: effects of exercise, age, and skeletal location. *American Journal of Physical Anthropology*, 116:266–277.
- Lieberman, D.E., Polk, J.D., Demes, B. (2004). Predicting long bone loading from cross-sectional geometry. *American Journal of Physical Anthropology*, 123:156-171.
- Macintosh, A.A., Davies, T.G., Ryan, T.M., Shaw, C.N., Stock, J.T. (2013). Periosteal versus

- true cross-sectional geometry: A comparison along humeral, femoral, and tibial diaphyses. *American Journal of Physical Anthropology*, 150: 442-452.
- Magennis, A. (1977). Middle and late archaic mortuary patterning: an example from the western Tennessee Valley. Master's Thesis, University of Tennessee.
- Martin, R.B., Burr, D.B, and Sharkey, N.A. (1998). *Skeletal Tissue Mechanics*. New York: Springer-Verlag.
- Marzke, M.W. (1997). Precision grips, hand morphology, and tools. *American Journal of Physical Anthropology*, 102:91-110.
- Marzke, M.W. and Shackley, M.S. (1987). Hominid hand use in the Pliocene and Pleistocene: Evidence from experimental archaeology and comparative morphology. *Journal of Human Evolution*, 15:439-460.
- Mays, S.A. (2002). Asymmetry in metacarpal cortical bone in a collection of British post-mediaeval human skeletons. *Journal of Archaeological Science*, 29: 435-441.
- McGrew, W.C. and Marchant, L.F. (1997). On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology*, 40:201–232.
- McGrew, W.C. and Marchant, L.F. (1999). Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates*, 40 (3): 509-513.
- McGrew, W.C. and Marchant, L.F. (2001). Ethological study of manual laterality in the chimpanzees of the Mahale Mountains, Tanzania. *Behaviour*, 138 (3): 329-358.
- O'Neill, M.C. & Ruff, C.B. (2004). Estimating human long bone cross-sectional geometric properties: A comparison of noninvasive methods. *Journal of Human Evolution*, 47, 221-235.

- Palastanga, N. and Soames, R.S. (2012). *Anatomy and Human Movement: Structure and Function*. Elsevier Ltd.
- Plato, C.C., Wood, J.L., and Norris, A.H. (1980). Bilateral asymmetry in bone measurements of the hand and lateral hand dominance. *American Journal of Physical Anthropology*, 52:27- 31.
- Roy, T.A., Ruff, C.B., and Plato, C.C. (1994). Hand dominance and bilateral asymmetry in the structure of the second metacarpal. *American Journal of Physical Anthropology*, 94:203-211.
- Ruff, C.B. (2000). Body size, body shape, and long bone strength in modern humans. *American Journal of Physical Anthropology*, 38: 269-290.
- Ruff, C.B. (2003). Long bone articular and diaphyseal structure in old world monkeys and apes. II: estimation of body mass. *American Journal of Physical Anthropology*, 120:16–37.
- Ruff, C.B. (2005). Mechanical determinants of bone form: insights from skeletal remains. *Journal of Musculoskeletal Neuronal Interactions*, 5 (3):202-212.
- Ruff, C.B. and Hayes, W.C. (1983). Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation: I. method and general patterns of variation. *American Journal of Physical Anthropology*, 60:359-381.
- Ruff, C.B. and Jones, H.H. (1981). Bilateral asymmetry in cortical bone of the humerus and tibia—sex and age factors. *Human Biology*, 53(1):69-86).
- Ruff, C.B., Walker, A., and Trinkaus, E. (1994). Postcranial robusticity in *Homo*. Ill: ontogeny. *American Journal of Physical Anthropology*, 93:35-54.
- Ruff, C.B., Holt, B., and Trinkaus, E. (2006). Who’s afraid of the big bad Wolff?: “Wolff’s

- law'' and bone functional adaptation. *American Journal of Physical Anthropology*, 129:484–498.
- Schultz, A.H. (1937). Proportions, variability, and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Human Biology*, 9 (3): 281-328.
- Stock, J.T. & Shaw, C.N. (2007). Which measures of diaphyseal robusticity are robust? A comparison of external methods of quantifying the strength of long bone diaphysis to cross-sectional geometric properties. *American Journal of Physical Anthropology*, 134, 412-423.
- Shaw, C.N. and Stock, J.T. (2009a). Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *American Journal of Physical Anthropology*, 140:149–159.
- Shaw, C.N. and Stock, J.T. (2009b). Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *American Journal of Physical Anthropology*, 140:160–172.
- Steele, and Uomini, N.T. (2005). Humans, tools and handedness. In V. Roux and B. Bril (Eds), *Stone Knapping: The Necessary Conditions for a Uniquely Hominin Behaviour* (217-239) Cambridge: McDonald Institute for Archaeological Research.
- Toth, N. (1985). Archaeological evidence for preferential right-handedness in the lower and middle Pleistocene, and its possible implications. *Journal of Human Evolution*, 14: 607-614.
- Trinkaus, E., Churchill, S.E., and Ruff, C.B. (1994). Postcranial robusticity in *Homo*. II: humeral bilateral asymmetry and bone plasticity. *American Journal of Physical Anthropology*, 93: 1-34.

- Trueman, C.N. and Martill, D.M. (2002). The long-term survival of bone: the role of bioerosion. *Archaeometry*, 44(3): 371-382.
- Uomini, N.T. (2009). The prehistory of handedness: Archaeological data and comparative ethology. *Journal of Human Evolution*, 57: 411-419.
- Wescott, D.J. (2006) Effect of mobility on femur midshaft external shape and robusticity. *American Journal of Physical Anthropology*, 130: 201–213.
- Westergaard, G.C. and Suomi, S.J. (1996). Hand preference for stone artefact production and tool-use by monkeys: possible implications for the evolution of right-handedness in hominids. *Journal of Human Evolution*, 30: 291–298.
- White, T.D. (2000) *Human Osteology*. San Diego: Academic Press.

APPENDIX

Table A1
Medians and means of MC2 %DA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{ep}/I_{min}	-0.518 (8.433)	-6.349 (-5.511)	31.678 (36.322)	-11.318 (-13.753)	-11.318 (0.299)	-10.558 (-24.292)	-6.236 (6.351)	3.277 (23.641)	-12.462 (-23.906)
I_{max}/I_{min}	3.822 (6.973)	-1.603 (3.591)	12.793 (13.738)	-11.428 (-8.326)	-9.838 (-0.138)	-12.78 (-14.467)	-2.619 (-1.155)	3.384 (2.555)	-10.549 (-7.647)
TA	-2.021 (-3.449)	-2.235 (-4.22)	1.434 (-1.907)	0.524 (1.182)	-1.47 (-5.423)	7.415 (6.136)	3.103 (4.434)	1.625 (2.19)	11.365 (8.362)
I_{ep}	-1.682 (1.079)	-4.169 (-9.583)	18.497 (22.405)	-6.047 (-5.233)	-6.047 (-10.361)	-1.839 (-1.388)	13.184 (16.623)	10.732 (27.704)	18.64 (-2.769)
I_{el}	-12.056 (-7.912)	-6.953 (-4.131)	-19.227 (15.473)	9.887 (8.659)	-8.171 (-10.844)	23.061 (23.287)	9.999 (11.573)	5.665 (6.05)	22.985 (21.238)
J	-3.443 (-5.85)	-4.459 (-7.74)	4.905 (-2.071)	1.415 (-3.85)	-8.975 (-22.438)	13.85 (10.091)	6.804 (9.033)	4.97 (5.122)	21.562 (15.879)
I_{max}	2.724 (-1.316)	-1.052 (-3.299)	9.095 (2.652)	3.572 (-1.836)	-4.698 (-10.448)	8.776 (4.623)	8.718 (8.69)	8.511 (6.043)	19.287 (13.322)
I_{min}	-5.853 (-8.383)	-5.989 (-7.114)	-3.709 (-10.921)	6.295 (6.34)	-8.108 (-10.458)	17.375 (18.939)	3.655 (9.817)	3.131 (3.481)	24.884 (20.906)

Table A2
Medians and means of MC2 %AA by site and by sex

Measure	Cherry Median %AA (mean %AA)			Eva Median %DA (mean %AA)			Ledbetter Landing Median %AA (mean %AA)		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
$I_{\text{L}}/I_{\text{L}}^{\text{min}}$	9.246 (19.675)	8.125 (11.249)	31.678 (36.529)	15.889 (24.211)	15.233 (18.551)	15.889 (28.457)	9.971 (29.677)	9.908 (30.976)	12.462 (27.405)
$I_{\text{max}}/I_{\text{min}}^{\text{max}}$	12.793 (16.029)	12.056 (17.174)	12.793 (13.738)	15.582 (18.574)	15.034 (16.443)	18.236 (20.172)	8.161 (8.906)	5.323 (8.078)	10.549 (10.354)
TA	6.977 (8.324)	3.756 (7.337)	7.745 (10.299)	7.459 (8.706)	1.652 (5.99)	9.413 (10.743)	4.351 (6.359)	3.103 (4.452)	11.365 (9.696)
$I_{\text{sp}}^{\text{sp}}$	8.023 (15.373)	6.088 (11.858)	18.497 (22.405)	16.856 (21.391)	11.546 (17.795)	18.951 (24.088)	19.189 (34.184)	13.184 (34.291)	22.573 (33.996)
$I_{\text{ml}}^{\text{ml}}$	16.826 (20.943)	12.07 (16.892)	19.227 (29.047)	18.389 (22.467)	12.372 (16.352)	23.061 (27.054)	12.992 (15.492)	9.999 (12.209)	22.985 (21.238)
J	8.92 (16.12)	7.064 (14.044)	15.825 (20.273)	17.741 (22.494)	8.975 (23.526)	20.034 (21.72)	9.489 (12.955)	6.804 (9.941)	21.562 (18.231)
I_{max}	9.78 (13.772)	6.731 (10.728)	16.942 (19.859)	14.759 (19.411)	10.795 (16.807)	17.909 (21.365)	12.404 (14.718)	8.718 (12.706)	19.287 (18.237)
$I_{\text{min}}^{\text{min}}$	13.926 (19.587)	9.104 (17.198)	19.688 (24.367)	12.762 (20.686)	9.186 (15.375)	21.689 (24.67)	9.799 (13.307)	7.413 (8.965)	24.884 (20.906)

Table A3
Medians and means of MC3 %DA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	9.844 (5.551)	0.668 (3.182)	19.188 (11.474)	4.309 (2.441)	8.665 (4.302)	-8.179 (0.581)	6.107 (3.114)	8.009 (-0.327)	4.482 (8.621)
I_{max}/I_{min}	7.642 (5.771)	6.065 (5.812)	8.656 (5.668)	2.38 (3.855)	6.007 (4.09)	-0.697 (3.619)	9.144 (10.598)	10.622 (7.564)	4.342 (15.452)
TA	1.244 (2.485)	0.24 (1.433)	8.399 (5.116)	3.046 (4.359)	6.202 (5.828)	2.475 (2.89)	3.387 (3.443)	3.552 (4.688)	3.387 (1.45)
I_{dp}	1.581 (7.832)	-0.43 (4.82)	15.509 (15.363)	4.21 (9.749)	16.639 (13.194)	11.78 (6.304)	10.088 (9.576)	10.333 (10.351)	7.297 (8.336)
I_{ml}	5.811 (2.377)	5.811 (1.738)	7.269 (3.977)	7.388 (7.359)	7.516 (9.092)	6.465 (5.625)	3.987 (6.451)	2.328 (10.677)	7.29 (-0.312)
J	3.125 (6.025)	-0.015 (3.934)	16.744 (11.252)	5.85 (8.969)	12.581 (11.792)	5.707 (6.147)	7.689 (8.578)	8.97 (10.516)	7.295 (5.477)
I_{max}	3.262 (7.848)	1.217 (5.715)	14.836 (13.181)	13.559 (10.341)	15.938 (13.176)	11.18 (7.506)	11.555 (12.331)	12.478 (13.298)	7.714 (10.786)
I_{min}	2.489 (2.177)	1.67 (0.032)	13.759 (7.539)	5.744 (6.517)	7.117 (9.208)	3.436 (3.826)	3.481 (1.726)	1.322 (5.738)	4.274 (-4.693)

Table A4
Medians and means of MC3 %AA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	17.219 (17.186)	13.627 (15.847)	21.769 (20.531)	13.664 (15.394)	16.148 (15.481)	13.365 (15.307)	12.653 (16.225)	12.683 (16.186)	12.38 (16.289)
I_{max}/I_{min}	11.57 (14.975)	11.57 (15.017)	13.476 (14.645)	9.632 (11.976)	9.227 (12.909)	10.037 (11.043)	12.099 (14.466)	12.918 (12.512)	5.349 (17.592)
TA	11.59 (9.175)	9.285 (8.417)	13.229 (11.069)	7.47 (8.739)	6.417 (9.645)	8.524 (7.832)	4.614 (5.86)	3.552 (4.688)	9.361 (7.736)
I_{dp}	15.687 (19.763)	14.068 (19.283)	15.687 (20.964)	21.264 (20.254)	21.587 (24.947)	16.652 (15.612)	10.088 (11.52)	10.333 (11.829)	7.297 (11.025)
I_{ml}	15.893 (18.965)	12.61 (17.223)	26.613 (23.32)	12.098 (18.344)	8.003 (15.947)	19.436 (20.742)	11.198 (15.961)	3.545 (12.423)	15.035 (21.62)
J	22.808 (19.188)	18.72 (18.192)	24.02 (21.679)	17.149 (18.041)	15.116 (20.204)	19.282 (15.877)	10.252 (12.167)	8.97 (10.516)	15.154 (14.809)
I_{max}	16.221 (19.888)	14.322 (20.135)	16.221 (19.269)	21.606 (20.694)	24.003 (24.363)	18.282 (17.026)	11.555 (13.373)	12.478 (13.298)	7.714 (13.494)
I_{min}	17.297 (17.765)	11.793 (14.807)	31.173 (25.159)	8.817 (16.601)	7.536 (14.944)	19.712 (18.257)	6.361 (11.71)	3.325 (7.601)	11.105 (18.285)

Table A5
Medians and means of MC4 %DA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	-0.649 (4.003)	-1.112 (7.533)	2.356 (-6.586)	-9.176 (-4.473)	-10.647 (-8.311)	11.181 (-1.489)	-4.075 (-6.852)	-17.571 (-12.733)	3.916 (4.911)
I_{max}/I_{min}	-0.431 (-0.939)	-2.888 (0.485)	6.022 (-5.21)	-6.775 (-2.206)	-18.295 (-4.961)	11.008 (-0.063)	-6.067 (-5.491)	-9.496 (-8.42)	-0.453 (0.367)
TA	6.122 (3.842)	6.465 (3.586)	2.411 (4.606)	11.702 (9.236)	8.633 (6.731)	12.08 (11.185)	10.524 (10.96)	10.493 (9.042)	13.533 (14.797)
I_{dp}	14.251 (8.896)	23.766 (9.817)	-10.12 (6.136)	17.018 (16.395)	26.808 (10.046)	16.895 (21.334)	19.442 (18.47)	16.01 (12.436)	34.375 (30.538)
I_{ml}	6.244 (5.011)	2.237 (2.335)	25.344 (13.041)	26.594 (20.586)	22.723 (17.906)	30.465 (22.669)	20.228 (25.185)	21.375 (24.955)	20.228 (25.646)
J	12.868 (7.54)	19.005 (7.249)	-0.626 (8.413)	23.501 (18.103)	16.025 (13.177)	24.495 (21.933)	20.8 (20.453)	19.922 (16.487)	28.155 (28.384)
I_{max}	8.812 (7.231)	23.977 (7.425)	-8.732 (6.651)	18.17 (17.25)	30.764 (11.243)	16.098 (21.923)	20.129 (18.84)	16.913 (13.916)	31.373 (28.689)
I_{min}	17.441 (8.324)	9.493 (7.036)	25.39 (12.188)	25.319 (19.19)	24.166 (15.897)	31.29 (21.752)	22.141 (24.18)	20.651 (22.143)	23.895 (28.255)

Table A6
Medians and means of MC4 %AA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	13.934 (18.224)	9.238 (17.44)	18.63 (20.577)	26.865 (26.399)	26.961 (26.959)	26.77 (25.951)	15.795 (14.431)	17.571 (17.998)	3.916 (7.298)
I_{max}/I_{min}	17.862 (20.999)	16.564 (20.666)	19.159 (21.997)	20.139 (24.283)	19.471 (23.392)	20.155 (24.976)	8.869 (10.461)	12.434 (13.335)	6.067 (4.714)
TA	7.593 (10.406)	8.704 (10.899)	6.482 (8.927)	13.228 (14.329)	14.377 (15.898)	12.08 (13.109)	10.524 (12.181)	10.493 (10.873)	13.533 (14.797)
I_{dp}	24.619 (22.943)	25.471 (22.783)	15.809 (23.422)	25.982 (28.708)	35.452 (35.814)	16.895 (23.181)	19.442 (22.62)	18.799 (18.661)	34.375 (30.538)
I_{ml}	19.238 (22.352)	13.132 (22.685)	25.344 (21.354)	30.565 (34.441)	30.666 (38.509)	30.465 (31.277)	20.228 (25.266)	21.375 (25.076)	20.228 (25.646)
J	19.362 (20.419)	19.72 (21.831)	11.029 (16.182)	24.651 (28.345)	30.767 (32.654)	24.495 (24.994)	20.8 (23.221)	19.922 (20.64)	28.155 (28.384)
I_{max}	24.27 (22.883)	24.562 (22.836)	15.83 (23.026)	26.654 (28.901)	34.779 (37.392)	16.098 (22.297)	20.129 (22.215)	17.657 (18.978)	31.373 (28.689)
I_{min}	25.649 (24.083)	26.797 (24.774)	25.39 (22.011)	30.656 (34.101)	26.472 (34.954)	31.29 (33.437)	22.141 (25.589)	20.651 (24.256)	23.895 (28.255)

Table A7
Medians and means of MC5 %DA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	-13.517 (-10.787)	-26.876 (-20.031)	-37.038 (-33.603)	6.354 (3.871)	-4.648 (-9.517)	29.255 (13.435)	-13.121 (-14.863)	-16.213 (-19.404)	3.301 (3.301)
I_{max}/I_{min}	0.676 (3.446)	-9.119 (-10.281)	-13.517 (-12.136)	-4.652 (0.071)	3.453 (1.181)	-5.186 (-0.722)	5.614 (6.825)	2.388 (6.133)	9.591 (9.591)
TA	-12.067 (-4.775)	1.971 (3.811)	0.676 (2.474)	6.052 (7.732)	4.132 (5.721)	7.966 (9.169)	4.226 (6.527)	8.541 (8.508)	-1.397 (-1.397)
I_{dp}	17.839 (19.063)	-14.393 (-2.342)	-11.381 (-11.263)	15.919 (16.909)	18.94 (6.165)	12.899 (24.584)	2.967 (5.445)	5.774 (6.919)	-0.451 (-0.451)
I_{ml}	1.785 (6.287)	16.26 (17.756)	21.833 (22.549)	21.538 (13.356)	4.688 (15.888)	23.5 (11.548)	16.257 (20.317)	24.634 (26.334)	-3.751 (-3.751)
J	1.711 (1.662)	2.998 (6.79)	1.785 (4.947)	12.171 (14.882)	9.085 (11.134)	16.297 (17.559)	7.889 (12.028)	17.425 (16.146)	-4.445 (-4.445)
I_{max}	8.079 (12.396)	-3.84 (2.375)	1.711 (-0.24)	19.763 (14.924)	10.538 (11.688)	22.246 (17.236)	11.972 (15.235)	22.75 (18.529)	2.057 (2.057)
I_{min}	33.054 (31.145)	9.403 (12.587)	8.079 (11.886)	11.668 (14.764)	7.092 (10.453)	23.497 (17.843)	2.798 (8.503)	9.918 (12.513)	-7.537 (-7.537)

Table A8
Medians and means of MC5 %AA by site and by sex

Measure	Cherry Median %AA (mean %AA)			Eva Median %DA (mean %AA)			Ledbetter Landing Median %AA (mean %AA)		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{nl}	33.054 (31.145)	30.066 (30.223)	37.038 (33.603)	27.546 (31.3)	24.361 (26.203)	33.227 (34.941)	13.121 (17.415)	16.213 (20.944)	3.301 (3.301)
I_{max}/I_{min}	13.517 (14.388)	14.421 (15.233)	13.517 (12.136)	8.802 (12.769)	8.326 (11.952)	9.279 (13.353)	9.591 (12.15)	9.691 (12.789)	9.591 (9.591)
TA	6.386 (7.57)	8.147 (9.481)	0.676 (2.474)	7.021 (10.872)	5.806 (8.044)	13.032 (12.893)	8.541 (10.221)	11.472 (12.427)	1.397 (1.397)
I_{dp}	24.558 (20.345)	26.109 (27.674)	11.381 (11.263)	21.715 (24.702)	21.999 (24.868)	12.899 (24.584)	9.846 (21.77)	15.547 (26.893)	1.281 (1.281)
I_{nl}	17.839 (20.345)	16.26 (19.518)	21.833 (22.549)	23.607 (24.033)	5.485 (18.082)	23.715 (28.283)	16.257 (21.817)	24.634 (26.334)	3.751 (3.751)
J	12.578 (15.304)	18.094 (19.188)	1.785 (4.947)	15.013 (20.953)	11.658 (15.797)	24.768 (24.636)	17.425 (21.114)	23.227 (25.281)	4.445 (4.445)
I_{max}	11.149 (16.729)	23.713 (2.729)	3.02 (3.395)	23.465 (21.379)	10.538 (16.445)	26.749 (24.902)	22.75 (22.573)	27.432 (27.703)	2.057 (2.057)
I_{min}	14.668 (17.021)	16.571 (18.946)	8.079 (11.886)	18.983 (20.97)	14.5 (16.253)	23.497 (24.339)	12.045 (18.74)	17.855 (21.54)	7.537 (7.537)

Table A9
Medians and means of Radius %DA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
$I_{\text{app}}/I_{\text{app}}$	-6.506 (-1.008)	-2.389 (1.741)	-6.506 (-6.506)	-10.622 (-13.148)	-10.58 (0.832)	-14.989 (-21.536)	-6.468 (-11.111)	-12.48 (-12.676)	7.343 (-9.546)
$I_{\text{max}}/I_{\text{min}}$	6.582 (2.036)	5.308 (-0.589)	7.285 (7.285)	8.265 (7.602)	5.426 (-0.736)	11.105 (12.605)	-2.537 (5.538)	-0.772 (6.43)	-8.043 (4.647)
TA	3.73 (7.463)	11.556 (11.209)	-0.028 (-0.028)	1.724 (-1.712)	7.003 (4.587)	1.402 (-5.492)	11.616 (12.573)	7.025 (7.645)	14.028 (17.501)
I_{app}	5.606 (13.987)	20.75 (23.132)	-4.304 (-4.304)	-11.633 (-10.164)	9.755 (9.235)	-18.065 (-21.803)	23.113 (18.921)	3.759 (9.41)	30.092 (28.431)
I_{app}	9.702 (14.898)	17.479 (21.238)	2.217 (2.217)	12.701 (3.091)	20.367 (8.35)	5.034 (-0.064)	23.6 (29.719)	22.939 (22.067)	24.261 (37.372)
J	21.173 (36.997)	37.25 (55.644)	-0.296 (-0.296)	3.665 (-2.212)	16.588 (9.003)	2.726 (-8.941)	22.242 (24.065)	17.478 (13.149)	27.691 (34.98)
I_{max}	10.845 (15.487)	18.406 (21.879)	2.705 (2.705)	6.409 (0.779)	21.601 (8.241)	4.17 (-3.698)	23.213 (25.61)	22.427 (15.623)	23.999 (35.597)
I_{min}	3.636 (13.471)	23.057 (22.5)	-4.586 (-4.586)	-5.268 (-7.219)	7.234 (8.993)	-14.008 (-16.946)	26.567 (20.346)	2.332 (9.202)	31.888 (31.49)

Table A10
Medians and means of Radius %AA by site and by sex

Measure	Cherry			Eva			Ledbetter Landing		
	Total	Males	Females	Total	Males	Females	Total	Males	Females
I_{dp}/I_{ml}	17.898 (18.623)	20.683 (22.424)	11.021 (11.021)	12.827 (19.083)	10.665 (14.995)	14.989 (21.536)	13.273 (18.247)	12.48 (12.676)	14.066 (23.819)
I_{max}/I_{min}	12.155 (11.026)	12.307 (12.896)	7.285 (7.285)	12.79 (19.778)	14.423 (13.969)	11.156 (23.264)	10.92 (14.51)	4.301 (9.812)	13.797 (19.207)
TA	3.758 (7.921)	11.556 (11.23)	1.303 (1.303)	5.907 (8.614)	7.715 (9.731)	2.682 (7.944)	11.616 (12.573)	7.025 (7.645)	14.028 (17.501)
I_{dp}	9.357 (17.717)	20.75 (23.132)	6.888 (6.888)	17.086 (18.88)	9.755 (14.009)	18.065 (21.803)	23.113 (18.921)	3.759 (9.41)	30.092 (28.431)
I_{ml}	9.702 (17.536)	17.479 (24.23)	4.149 (4.149)	24.685 (24.465)	30.77 (28.864)	21.451 (21.826)	23.6 (29.719)	22.939 (22.067)	24.261 (37.372)
J	21.173 (37.276)	37.25 (55.644)	0.54 (0.54)	12.518 (18.021)	20.445 (22.634)	6.723 (15.253)	22.242 (24.324)	17.478 (13.668)	27.691 (34.98)
I_{max}	10.845 (15.487)	18.406 (21.879)	2.705 (2.705)	25.799 (24.455)	29.997 (28.239)	8.649 (22.185)	23.213 (26.348)	22.427 (17.099)	23.999 (35.597)
I_{min}	7.435 (16.528)	23.057 (22.5)	4.586 (4.586)	11.041 (16.118)	8.074 (14.375)	14.008 (17.163)	26.567 (20.346)	2.332 (9.202)	31.888 (31.49)