

1 **Biomechanical Investigation of Ancient Maya Warfare at Mayapan, Yucatan, Mexico**

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25 Running head: Biomechanical investigation of Maya warfare

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31 **Abstract**

32 Despite significant advancements in the reconstruction of activity patterns from skeletal remains and  
33 growing scholarly interest in ancient warfare, few biomechanical studies have investigated weaponry use.  
34 We adopt a biomechanical approach to investigate who participated in ancient Maya warfare and the  
35 types of weaponry used at the Late Postclassic (ca. 1200-1450 A.D.) regional political capital of Mayapán  
36 located in northwestern Yucatán, Mexico. This has implications for the nature and scale of Maya warfare  
37 and the size of territories that could be controlled by Maya polities. Comparative Finite Element Analysis  
38 is a powerful, non-destructive method that can be applied to skeletal remains to model strain, stress and  
39 deformation of structures in response to a defined loading regime. Here, biomechanical data extracted  
40 using cross-sectional geometry were combined with Finite Element Analysis models of three ancient  
41 Maya humeri from Mayapán: one elite male, one elite female, and one commoner female. Models were  
42 created with loading conditions of archery and spear use to assess evidence for skeletal adaptation to  
43 habitual weapon use. Following suggestions by some Mayanists that elite status males were the principal  
44 participants in warfare, we hypothesized that the elite male humerus would exhibit lower strains than the  
45 two female humeri in all the loading conditions. This was supported by the Finite Element model results,  
46 with the exception of spear throwing. The elite female humerus showed similar trends to the elite male  
47 humerus, suggesting the possibility of elite female participation in warfare.

48

49 **Keywords:** bone, warfare, upper limb biomechanics, cross-sectional geometry, bone function adaptation

50

## 51 **1. Introduction**

52 The daily lives of ancient populations continue to be of interest to researchers. Over the last several  
53 decades, there has been an increase in studies investigating activity patterns and lifestyle in ancient human  
54 skeletal remains (Jurmain, 2013; Ruff, 2018). Studies of ancient populations and contemporary  
55 professional athletes indicate that different activities impose varying degrees and kinds of observable  
56 stress on human bone (Alves Cardoso & Henderson, 2010; Keeley, Hackett, Keirns, Sabick, & Torry,  
57 2008; Lai & Lovell, 1992; Larsen, 2015; Nissen et al., 2007; Villotte et al., 2010). These studies are  
58 underpinned by the idea of functional bone adaptation, which suggests that a bone will modify itself in  
59 response to stresses and strains applied to it through repetitive and frequent strenuous activities or  
60 external stresses (Panagiotopoulou, 2009; Ruff, Holt, & Trinkaus, 2006; Ruff, 2018). Several different  
61 approaches have been used to reconstruct activity patterns in past populations from the human skeleton,  
62 including analyses of external bone dimensions and cross-sectional geometry (Bridges, 1989; Cole, 1994;  
63 Larsen, 2015; Ruff, 2008; Ruff & Hayes, 1983a, 1983b; Stock & Pfeiffer, 2004; Wanner, Sosa, Alt, &  
64 Tiesler, 2007; Wescott, 2006). These approaches are typically applied to long bone diaphyses, which have  
65 been shown to be the most reflective of habitual behavior and useful for illustrating mechanical  
66 adaptation, capturing the responsiveness of cortical bone to different loading regimes (Auerbach & Ruff,  
67 2006; Buck, Stock, & Foley, 2010; Lieberman, Devlin, & Pearson, 2001; Ruff et al., 2006), evidenced  
68 through clinical research and studies on modern athletes, among others (Biewener & Bertram, 1994; Burr,  
69 Robling, & Turner, 2002; Carlson, 2005; Carlson, Grine, & Pearson, 2007; Jones, Priest, Hayes,  
70 Tichenor, & Nagel, 1977; Ruff & Runestad, 1992; Shaw, 2011; Shaw & Stock, 2009a, 2009b). Therefore,  
71 analyzing the morphology of certain skeletal elements permits reconstruction of loading patterns and  
72 lifestyles in the distant past (Knüsel, 2000; Ruff, 2008; Stock & Pfeiffer, 2001).

73  
74 Recent studies reconstructing ancient Maya activity patterns have focused on skeletal adaptations  
75 reflecting habitual participation in agricultural, food preparation and administrative activities, as well as  
76 canoeing, trauma and sexual division of labor, in populations from the Classic period (ca. AD 300-1000)  
77 (Maggiano et al., 2008; Nystrom, Buikstra, & Braunstein, 2005; Nystrom & Buikstra, 2005), whereas  
78 activity patterns in other time periods, including the Postclassic period (ca. AD 1000-1524), have received  
79 less attention (but see Arias López et al 2014, 2022). In much of the Maya area, the transition from  
80 Classic to Postclassic period was a time of significant culture change which may have been brought about  
81 in part by drought, warfare, migration and political economic reorganization reflecting growing  
82 importance of long distance coastal trade networks, although certain regions show greater continuity and  
83 even flourished during this time, notably parts of northern Belize, the Caribbean coast of Mexico and  
84 highland Chiapas (Aimers, 2007; Demarest & Rice, 2005; Douglas et al. 2015; Turner & Sabloff, 2012).

85 Militarism is traditionally thought to have increased during the Postclassic, though recent research  
86 demonstrates the important role of warfare in cultural developments throughout Maya history (Canuto et  
87 al. 2018; Inomata, 2014; Wahl, Anderson, Estrada-Belli, & Tokovinine, 2019).

88  
89 Nevertheless, many questions remain regarding Maya warfare, how it changed through time and the  
90 impact of these changes on the wider society (Aoyama & Graham, 2015; Inomata, 2014; Scherer et al.,  
91 2022; Stanton, 2019; Webster, 2000). One of the most pressing of these is who actually participated in  
92 war. It remains unclear as to whether Maya warfare was waged mainly by elite males (Aoyama and  
93 Graham, 2015; Freidel, 1986) or included widespread participation of commoners and other segments of  
94 the population (Scherer et al., 2022:22; Stanton, 2019:216; Webster, 2000). This has numerous  
95 implications, not least the scale of Maya warfare and the size of territories that could be controlled by  
96 Maya polities. Estimates of the number of combatants that could be fielded by a large polity vary from a  
97 few hundred into the tens of thousands (Stanton, 2019:216). Recent discoveries of large-scale  
98 fortifications and sitewide destruction certainly suggest that warfare could, at times, impact all members  
99 of a given settlement (Canuto et al., 2018; Wahl et al., 2019). Elite female participation in warfare has  
100 been suggested based on decipherments of Maya hieroglyphic writing and depictions of queens as  
101 warriors (Ardren, 2002; Reese-Taylor, Mathews, Guernsey, & Fritzler, 2009). In addition, healed and  
102 unhealed skeletal trauma identifying particular females as victims of violence have been reported (e.g.,  
103 Hooton, 1940; Nystrom and Buikstra, 2005; Serafin et al., 2014; Tiesler and Cucina, 2012), but  
104 convincing evidence that females served as combatants in organized violence has yet to be found.

105  
106 Another important yet understudied question is what weapons were used in warfare and how this changed  
107 through time (Aoyama, 2005; Roche Recinos et al., 2021; Scherer et al., 2022; Stanton, 2019). Part of the  
108 difficulty lies in the fact that tools could have served multiple purposes, which also contributes to the  
109 challenge of identifying warriors based on associated grave goods. Spears, atlatls and bows and arrows  
110 may have been used for hunting, warfare or both. Likewise, axes may have served for felling trees or for  
111 combat. Clubs and sword-like implements of perishable materials may also have been used but the  
112 evidence at present is largely limited to indirect ethnohistoric and artistic sources (Abtosway and  
113 McCafferty, 2019; Hassig, 1992; Rice, 2022). Art rarely portrays commoners and may present idealized  
114 depictions that did not necessarily reflect reality (Abtosway and McCafferty, 2019; Stanton, 2019). For  
115 example, studies of chipped stone tools in lithic assemblages from Copan and Ceibal show that spear  
116 points predominated from the Middle Preclassic (1000-300 BC) until the Terminal Classic (AD 800-  
117 900/1000) when atlatl dart points and arrowheads increase notably in frequency (Aoyama & Graham,  
118 2015). The latter become particularly common in the Late Postclassic (Escamilla Ojeda, 2004; Masson

119 and Peraza Lope, 2014; Simmons, 2002), yet bows and arrows were rarely rendered in art during any  
120 period. Similarly, caches of round stones for throwing or hurling with slings have been recovered in Late  
121 Preclassic (300 BC – 300 AD) and Late Classic contexts at Usumacinta region sites (Roche Recinos et al.,  
122 2021). These weapons are little known from artistic depictions of warfare but are common in  
123 ethnohistoric accounts of conflict between Spanish and Maya in the early colonial period. Notably,  
124 slingstones would have been accessible to a large swath of the populace and required less training  
125 compared with other weapons, as may also have been true to some extent for bows and arrows (Hassig,  
126 1992:156; Roche Recinos et al., 2021).

127  
128 The reconstruction of activity patterns from skeletal remains has the potential to shed new light on who  
129 participated in ancient Maya warfare (Stanton, 2019:217) as well as the weapons they may have used. A  
130 small but growing number of biomechanical studies have investigated weaponry use (Ogilvie & Hilton,  
131 2011; Rhodes & Churchill, 2009; Rhodes & Knüsel, 2005). Studies applying traditional morphometrics  
132 have advanced our knowledge of the interrelationship between form and function, however computational  
133 modeling approaches enable more complex differences in morphology to be assessed (McCurry et al.,  
134 2015). Finite element analysis (FEA) is a computational method that enables strain, stress and  
135 deformation of structures to be modeled in response to a defined loading regime (Rayfield, 2007),  
136 allowing one to comprehensively map and model strain throughout the entirety of the structure. This  
137 method uses numerical methods to predict how a complex structure, bone in this case, responds to applied  
138 loads. As such, FEA is an ideal, non-destructive approach for modeling how skeletal elements respond to  
139 different mechanical forces. Here we adopt a comprehensive, combined analytical approach to assess  
140 biomechanical hypotheses, using both FEA and cross-sectional biomechanical property data extracted  
141 from segmented computed tomography (CT) data. Cross-section biomechanical property data have been  
142 used extensively in studies of past and present populations to assess evidence for bone functional  
143 adaptation associated with mobility and habitual activity, including behaviors engaging the upper limb  
144 (e.g., throwing and swimming) (e.g., Shaw & Stock, 2009). With this quantitative approach, we aimed to:

- 145 1) Examine the effects of differences in humeral diaphyseal structure between Maya individuals of  
146 different sex and social status on the location and magnitude of strain.
- 147 2) Determine whether Maya individuals of different sex and social status possessed humeri that  
148 could perform better at behaviors used in warfare.

149  
150 The sample consisted of computed tomography (CT) scans of three left humeri dating to the Late  
151 Postclassic Period from the archaeological site of Mayapán, Yucatán, Mexico. Mayapan was a regional  
152 political capital during the Late Postclassic period that unified much of northwestern Yucatán and exerted

153 more indirect influence further afield (Masson and Peraza Lope, 2014). Militarism was an important tool  
154 of political control throughout its occupation (Kennett et al., in press) making it an ideal site at which to  
155 investigate who participated in Postclassic Maya warfare and how it was conducted. The three left humeri  
156 scanned pertain to an elite male (Burial 32) who was likely a warrior, an elite female (Burial 21) and a  
157 probable commoner female (Cenote Sac Uayum 190). In light of the preponderance of arrowheads in Late  
158 Postclassic contexts, for the elite male humerus we would expect lower levels of strain under simulated  
159 conditions of archery compared with spear use. Further, as it is a left humerus, we would expect less  
160 strain when simulating the bow arm as opposed to the draw arm as the bow arm is typically the non-  
161 dominant arm, which is the left arm in most individuals, while the dominant arm, which is the right arm  
162 in most individuals, is responsible for the drawing of the bow (Dorshorst, 2019; Hayri Ertan, Knicker,  
163 Soylu, & Strüder, 2011; Simsek, Cerrah, Ertan, & Soylu, 2018; Stock, Shirley, Sarringhaus, Davies, &  
164 Shaw, 2013). Likewise, when modeling spear use, it is expected that the forward arm will show lower  
165 magnitudes of strain compared with the trailing arm. The commoner female likely led a more physically  
166 demanding lifestyle overall compared with the elite female. This may have included a variety of activities  
167 such as grinding maize, which would have placed similar stresses on both upper limbs. Therefore, we  
168 would also expect lower strain levels in the commoner female compared with the elite female, though  
169 elite females are thought to have played important roles in craft production (Aoyama, 2017; Aoyama &  
170 Graham, 2015; Ardren, 2002; Reese-Taylor et al., 2009; Wahl et al., 2019; Walden et al., 2019; Wanner  
171 et al., 2007). As such, we hypothesized that the male humerus would exhibit lower levels of strain under  
172 the simulated conditions of archery and spear use in comparison to the female humeri.

173

## 174 **2. Materials and Methods**

### 175 **2.1 Bone Selection and Mesh Generation**

176 The five humeri analyzed in this study are curated in the laboratory of the Proyecto Mayapán, which is  
177 directed by archaeologist Carlos Peraza Lope of the Instituto Nacional de Antropología e Historia (INAH)  
178 of Mexico. This project received approval from UNSW Human Ethics, under the negligible risk pathway,  
179 appropriate for Archaeological projects that involve historical bone specimens (ID: HC210220). The  
180 humeri were scanned using computed tomography (CT). Scans were conducted using a GE Lightspeed  
181 VCT XT 128-slice CT scanner at a resolution of 0.6mm x 0.6mm. The three most complete, all from the  
182 left side, were chosen for Finite Element Analysis (Table 1). The CT data for the three humeri were  
183 digitally segmented in MIMICS Research v. 20.0 (Materialise NV, Leuven, Belgium), to create surface  
184 models of the humeri. These models were converted into solid tetrahedral (tet4) models, composed of  
185 approximately 200,000+ brick elements for each humerus, with a triangle edge length of 2.8 mm.

186 Meshing was conducted using 3-Matic Research v. 9.0 (Materialise NV, Leuven, Belgium) and volume  
187 meshes were exported as Nastran (.nas) files.

188

## 189 **2.2 Cross-sectional geometry**

190 Virtual cross sections were extracted from 3D humeri bone models using the method introduced by  
191 Wilson and Humphrey (2015). The three complete humeri used for the Finite Element Analysis were  
192 sampled, as well as two contralateral (right) elements, corresponding to the right humerus of H10 (elite  
193 male, H11) and H15 (elite female, H14) (Tables 1, 2). The two right humeri had minor damage to the  
194 condyles and were aligned to their corresponding, undamaged left sides using principal axis alignment in  
195 Rhinoceros 5 Software (McNeel & Associates 2022), to enable cross section extraction (see Wilson &  
196 Humphrey, 2015). Cross sections were extracted at the midshaft (50%), capturing both endosteal and  
197 periosteal geometry information provided by the computed tomography data, as bending load is highest in  
198 this region of the diaphysis (Ruff, 2000). The engineering principle of ‘Beam Theory’ is a common  
199 method used in biomechanics to determine the robusticity of human long bone (Ruff & Hayes, 1983). By  
200 calculating specific geometric values an understanding of the mechanical properties and loading abilities  
201 of a bone is developed (Ruff, 2000). Standard measurements comprise cortical area (CA) a measure of  
202 compressive strength, total subperiosteal area (TA) the total combined value of cortical bone and  
203 medullary area; second moments of area along the x and y axes ( $I_x$ ,  $I_y$ ) and the maximum and minimum  
204 second principal of area ( $I_{max}$ ,  $I_{min}$ ) which is correlated to maximum and minimum bending strength  
205 (Davies et al 2012). From these standard measurements additional values can be calculated including a  
206 measure of torsional strength through the second polar moment of area ( $J = I_x + I_y$ ), an estimate of the  
207 distribution of cortical bone in the form of a ratio ( $I_{max}/I_{min}$ ); and the estimate of distribution of cortical  
208 bone along the x and y axes ( $I_x/I_y$ ) (Nystrom & Buikstra, 2005). Following other comparative studies of  
209 cross-sectional geometry (e.g., Shaw & Stock, 2009) and to facilitate comparison with published values,  
210 CA, TA and J values were corrected for body mass, using a formula from Ruff et al. (2020), based on  
211 humeral head diameter measurements (Ruff, Squyres, & Junno, 2020) (Tables 1-2).

212

## 213 **2.3 Finite Element Modeling**

214 Finite element modeling was undertaken in Strand7 (V2.4.6), using the linear static solver. We assumed  
215 bone to be elastic, behaving in a linear fashion, allowing a proportionate stress/strain relationship. Bone  
216 material properties are typically anisotropic and heterogeneous (Berthaume, 2014; Currey, 2006; Rho,  
217 Kuhn-Spearing, & Zioupos, 1998; Strait et al., 2005), however taphonomic phenomena can distort the  
218 quality and material properties of bones. Following previous comparative FEA studies, we assume that all  
219 three humeri had analogous material properties and any error introduced to the models by assigning

220 homogeneous, isotropic material properties is negligible (Berthaume, 2014; Wroe et al., 2018). We  
221 assigned a Young's modulus of 17.2 GPa and a Poisson's ratio of 0.3 (Currey, 2006; Zadpoor, 2006).  
222 To facilitate assignment of muscle attachment sites, muscle beams, and boundary conditions, a CT scan of  
223 a *Homo sapiens* scapula, ulna and radius was used as a scaffold, oriented in space around each humerus in  
224 anatomical position. These elements were sourced from Morphosource (<https://www.morphosource.org>)  
225 and downloaded as .ply files before being exported as STL files using Meshlab (ISTI-CNR, Tuscany,  
226 Italy).

227

228 Five loading regimes were used to stimulate forces of various phases during archery and spear use. These  
229 were: 1) Archery bow arm, 2) Archery draw arm, 3) Spear throwing, 4) Spear thrusting forward arm, and  
230 5) Spear thrusting trailing arm. The first 2 loading cases modeled the bones during archery, for both the  
231 bow arm and draw arm. One cycle of archery consists of 3 phases; Start phase, full draw phase, and  
232 release phase (Ahmad et al., 2014; Dorshorst, 2019; Reddy, 2015). This study used the full draw phase  
233 (Fig. 1A) for its modeling of archery as it has been shown to have the highest percent (%) maximum  
234 voluntary contractions and peak muscle activation (Ahmad et al., 2014; Dorshorst, 2019; Pontzer et al.,  
235 2017; Reddy, 2015; Woods, Robertson, Rudd, Araujo, & Davids, 2020). The positioning of the bones for  
236 each loading regime was achieved by incrementally moving the models into the correct anatomical  
237 position individually, relative to the humerus. The bow and draw arm involved varying degrees of  
238 abduction, adduction and extension at the shoulder joint, and flexion and extension at the elbow joint  
239 (Dorshorst, 2019; Pontzer et al., 2017).

240

241 For spear use, both spear throwing and spear thrusting loading cases were modeled and used. For spear  
242 throwing, this study modeled the bone positions after the maximum level of muscle activity during the  
243 acceleration phase (Fig. 1B) (Illyes & Kiss, 2005; Reddy, 2015; Roach, Venkadesan, Rainbow, &  
244 Lieberman, 2013; Sabick, Kim, Torry, Keirns, & Hawkins, 2005). Spear throwing mainly involves  
245 external rotation of the humerus, abduction at the shoulder joint, and flexion at the elbow joint (Dorshorst,  
246 2019).

247

248 For spear thrusting, two loading cases were used, modeling both the forward arm and trailing arm. The  
249 highest point of muscle activity at the end of the thrusting cycle was used for the models in this study  
250 (Aoyama, 2005; Berthaume, 2014) (Fig. 1C). Spear thrusting involves abduction, adduction, flexion and  
251 extension at the shoulder joint, and flexion at the elbow joint (Ahmad et al., 2014; Berthaume, 2014;  
252 Maki, 2013).

253



## 254 **2.4 Boundary Conditions**

255 The X, Y, and Z axes were preserved from CT scanning, such that the humeri were oriented relative to the  
256 global coordinate system in Strand7. The humeri had zero-displacement constraints applied both  
257 proximally and distally, mimicking forces and articulation from the glenoid fossa, ulna and radius.  
258 Distally, the humerus was fixed against translation and rotation in all three axes over the area of the  
259 humeroulnar and humeroradial joints. Proximally, the humerus was fixed at two nodes, the first being  
260 placed over the area of the glenohumeral joint in all three directions, preventing translation or expansion  
261 within the joint, and the second node at the center of the head of the humeri in all three directions in order  
262 to replicate forces from the glenoid fossa (Berthaume, 2014; McCurry et al., 2015; Stein et al., 2020).

263

## 264 **2.5 Loading Conditions**

265 Muscles were simulated in the models as beam elements with the property of structural steelwork and  
266 were assigned a geometric diameter of 0.5 millimetres (McCurry, Walmsley, Fitzgerald, & McHenry,  
267 2017; Panagiotopoulou, 2009; Stein et al., 2020). Locations of muscle attachment sites were chosen based  
268 on previous publications in human anatomy (Alves Cardoso & Henderson, 2010; Apreleva, Ozbaydar,  
269 Fitzgibbons, & Warner, 2002; Buck et al., 2010; Quental, Folgado, Ambrósio, & Monteiro, 2012; Robb,  
270 1998; Standring, 2021; Zumwalt, 2006). A network of beams was tessellated around the location of each  
271 muscle beam attachment site to minimize anomalous stress values associated with single node loadings  
272 (Attard et al., 2016). The beams at the attachment sites were also given the property of structural  
273 steelwork, with a geometric diameter of one millimetre (Stein et al., 2020). Muscle beams were linked  
274 from the centre of each attachment site on the respective bone. These muscle beams then had forces  
275 applied to them while the bones were in anatomical position. The forces applied were calculated using a  
276 Hill-type muscle model (Zajac, 1989) using parameters derived from previous anatomical studies (An,  
277 Hui, Morrey, Linscheid, & Chao, 1981; Garner & Pandy, 2001; Holzbaur, Murray, & Delp, 2005;  
278 Langenderfer, Jerabek, Thangamani, Kuhn, & Hughes, 2004; Lieber, Jacobson, Fazeli, Abrams, & Botte,  
279 1992; Murray, Buchanan, & Delp, 2000; Zajac, 1989) (Table 3). Body mass estimates showed a  
280 maximum difference of approximately 14% between all three humeri, which aligns with comparisons of  
281 other humeral measurements, including humeral length. Since body mass estimates were similar for all  
282 individuals, muscle forces were not scaled, as it would not have made a material difference to the results  
283 (Ruff et al., 2020) (Table 1).

284

285 The accompanying Newtons (N) of force that were applied to each muscle beam are shown in Table 4.  
286 The pectoralis major and latissimus dorsi muscles were excluded due to their low relative engagement for  
287 the respective actions compared to the other muscles being modeled (Berthaume, 2014; Dorshorst, 2019;

288 Woods et al., 2020), coupled with the difficulty of mapping these muscles due to requiring additional  
289 bone CT scans to accommodate the attachment sites for these muscles. This would greatly increase the  
290 difficulty of the modeling, as well as the risk for inaccuracies due to requiring manual positioning of  
291 elements (Krings, Marce-Nogue, Karabacak, Glaubrecht, & Gorb, 2020; Panagiotopoulou, 2009; Ruff et  
292 al., 2006; Zhang et al., 2021).

293

294 The Strand7 files for the bone models that were in anatomical position had boundary and loading  
295 conditions applied and were then duplicated for each model. Each duplicate went through manual,  
296 incremental movement of the scapula, radius, and ulna, to align the bones with the position that would be  
297 present during the action being modeled (Fig1A-C), with the humeri remaining in place. Qualitative  
298 visual comparisons were generated using color-contour maps for each model, showcasing the von Mises  
299 (VM) brick stresses outputted from the model solve, present along the anterior and posterior of each  
300 humerus. In addition to these visual comparisons, 95% VM brick stress values of the models were  
301 generated using R code from McCurry et al (2015) and Walmsley et al (2013) (Supplementary Material  
302 1). These values were displayed using histograms, which were generated using GraphPad PRISM 9.0.  
303 The 95% values represent global strain for the model whilst reducing the impact from artefacts at sites of  
304 attachment, loading and constraints, which would usually represent the peak strain values within models  
305 (McCurry et al., 2015; McCurry et al., 2017; Panagiotopoulou, 2009; C. Ruff et al., 2006; Stein et al.,  
306 2020; Walmsley et al., 2013).

307

### 308 **3. Results**

#### 309 **3.1 Biomechanical properties extracted from humeral cross sections**

310 Cross-sectional geometry data were extracted from the same models that were used in Finite Element  
311 Analysis (H10, H15, H30) plus the right side for H10 (H11) and the right side for H15 (H14). This  
312 enabled a simple description of asymmetry in left and right sides to be extracted. All samples showed  
313 greater bending strength in the anterior-posterior plane with a more ovoid diaphyseal shape, evidenced by  
314  $I_x/I_y$  values much greater than 1.0 (Table 2), with the elite female (H15) showing the highest values for  
315  $I_x/I_y$ . Overall, the elite male and elite female humeri were shown to have greater resistance to torsional  
316 stress and greater overall robusticity than the commoner female humerus (H30). The cortical and total  
317 area as well as torsional rigidity value (CA, TA, J) show that the elite male sample exhibits higher values  
318 pertaining to overall bone strength and capacity to resist stress, in comparison to the elite and commoner  
319 female (Table 2).

320

321 Differences between left and right (Table 5) sides indicated a 7-9% difference in total area (TA) values,  
322 indicating a right-hand bias in the elite sample. Differences between left and right cortical area (CA) were  
323 greater for the elite male (H10, H11) (5%) compared to the elite female (H14, H15) (<1%), indicating  
324 more pronounced asymmetrical resistance to torsional strain in the elite male.

325

### 326 **3.2 Archery Bow Arm Models**

327 During the archery bow arm loading scenarios, the humerus H10 model experienced the lowest levels of  
328 strain and H30 the highest (Fig. 2). The bulk of the strain can be seen to occur near the midshaft and  
329 proximal shaft of the anterior part for all humeri. H30 also shows, uniquely, greater strain at the  
330 anterodistal end of the shaft, adjacent to the trochlea (Fig. 2C). The strain on the anterior side of H15  
331 between the proximal shaft and midshaft is more spread out in comparison to H10 and H30. H10  
332 experienced comparatively lower levels of strain at the distal end of the shaft both anteriorly and  
333 posteriorly, while H15 and H30 experienced greater strains.

334

### 335 **3.3 Archery Draw Arm Models**

336 During the archery draw arm loading scenarios, H10 also experienced the lowest strain values. In contrast  
337 with the bow arm models, H15 had higher peak values than H30, although the differences were small  
338 (Fig. 3). The bulk of the strain can be seen to occur at the midshaft, both anteriorly and posteriorly, for all  
339 humeri (Fig. 3A-C). H15 displayed great strain at the proximal shaft anteriorly and just beneath the  
340 humeral head at the level of the surgical neck. H30 also showed strain at the proximal shaft anteriorly but  
341 H10 did not. H15 also displayed greater stress at the humeral head in comparison to both H30 and H10.

342

### 343 **3.4 Spear Throwing Models**

344 During the spear throwing loading scenarios, H15 was shown to have the highest strain values, followed  
345 by H10 and H30 (Fig. 4). All three models show very high levels of strain throughout the entirety of the  
346 humerus, grossly generating more bone shaft strain, extending to the humeral head, with the distal end  
347 showing comparatively smaller magnitudes of strain (Fig. 4A-C). However, the strain shown at the  
348 humeral head for H30 is lower in comparison to H10 and H15.

349

### 350 **3.5 Spear Thrusting – Forward Arm Models**

351 During the spear thrusting – forward arm loading scenarios, humerus H10 experienced the lowest levels  
352 of strain and H30 the highest (Fig. 5). The bulk of the strain can be seen to occur near the midshaft and  
353 proximal shaft of the anterior part for all humeri, as was also the case for the bow arm models, but with  
354 the strain being spread more evenly from the proximal to the distal ends of the shaft, both anteriorly and

355 posteriorly in the spear thrusting forward arm models. H30 also shows great strain at the distal end of the  
356 shaft anteriorly, adjacent to the trochlea (Fig. 5C). The strain on the anterior of H15 between the distal  
357 shaft and midshaft is more spread out in comparison to H10 and H30. H10 and H15 experienced  
358 comparatively lower levels of strain posterodistally in comparison to H30, while H15 and H30  
359 experienced greater strains anterodistally in comparison with H10.

360

### 361 **3.6 Spear Thrusting – Trailing Arm Models**

362 During the spear thrusting – trailing arm loading scenarios, humerus H10 experienced the lowest levels of  
363 strain and H30 the highest (Fig. 6). The differences between peak VM strain values are comparatively  
364 lower compared to the archery bow arm and spear thrusting forward arm cases (Fig. 6D). The bulk of the  
365 strains for all models can be seen to occur at the midshaft both anteriorly and posteriorly. H10 shows  
366 lower strain at the proximal shaft adjacent to the surgical neck anteriorly and posteriorly compared to H15  
367 and H30. H30 shows increased strain anterodistally in comparison to H10 and H15.

368

### 369 **3.7 Bone Comparisons**

370 Spear throwing loading cases have the highest peak strain value, with the archery draw arm and spear  
371 thrusting forward arm having the lowest peak strain values (Fig. 7). H10 showed the lowest peak strain  
372 values for all loading scenarios (Fig. 7A) except for spear throwing, while H30 showed the highest peak  
373 value strains, with the exception of spear throwing and the archery draw arm (Fig. 7C). H15 shows  
374 similar trends in comparison to H10. Although the values shown for H30 do not fit into the trends  
375 displayed by the other two humerus models, the peak strain values shown for all loading cases for H30  
376 are closer together with smaller differences (Fig. 7D).

377

## 378 **4. Discussion**

379 Finite Element Analysis (FEA) has rarely been applied in bioanthropological investigations of weaponry  
380 use and has not been applied at all to studies of the Maya, despite growing interest in ancient Maya  
381 warfare. Here, FEA was used to analyze Maya humeri to advance knowledge regarding the use of  
382 weapons in ancient Maya populations.

383

384 Archery and spear use (for thrusting) are bimanual activities, where each arm performs different  
385 movements, resulting in different levels of muscle activations even if the same muscle groups are used  
386 (Peterson, 1998). Research suggests that such bimanual activities could be associated with decreased  
387 asymmetry between humeri (Dorshorst, 2019; Rhodes & Knüsel, 2005; Thomas, 2014), as mechanical  
388 loads are placed on both the dominant and non-dominant arms. This implies that if one is undertaking

389 bimanual activities habitually then both left and right sides, regardless of which arm is dominant, should  
390 exhibit lower stress under loading conditions associated with archery. Therefore, the relative magnitude  
391 of difference between the bow arm and draw arm loading scenarios, i.e., the difference in stress on the  
392 same bone from the same individual under the bow arm vs draw arm loading scenarios, should be smaller  
393 in the individuals who, we expect, performed this behavior frequently, i.e., the elite male, as compared to  
394 the elite and commoner females. This is partially supported by the present study. H10, the elite male  
395 humerus, and H30, the commoner female humerus, show a greater magnitude of difference between  
396 loading cases, except for spear throwing. Comparing H10 with H15, the elite female humerus, the smaller  
397 relative magnitude of difference between loading cases may indicate a similar undertaking of certain  
398 behaviors. Further studies should use methods such as FEA on both left and right humeri in order to test  
399 the hypothesis, augmenting the asymmetry values recorded on the elite male and female in this sample  
400 (Table 5). Movements involving adduction/abduction have been shown to apply medio-lateral bending in  
401 the humerus, with flexion/extension resulting in antero-posterior bending (Dorshorst, 2019; Rhodes &  
402 Knüsel, 2005; Ruff, 2018). Electromyography data shows that for the bow arm, the triceps brachii has the  
403 highest peak muscle activation, followed by the biceps brachii in the draw arm, which would both result  
404 in anterior-posterior bending (Dorshorst, 2019; Ertan et al., 2011; Ertan, Soylu, & Korkusuz, 2005; Lin et  
405 al., 2010). This would increase the robusticity of the non-dominant arm, supporting the hypothesis that  
406 bimanual activities reduce humeral asymmetry. The bow arm model strain is indicative of a combination  
407 of humeral torsion and antero-posterior bending, which is consistent with evidence that the bow arm in  
408 archery results in antero-posterior bending as well as medio-lateral bending, with some humeral torsion  
409 (Dorshorst, 2019; Rhodes & Knüsel, 2005). H10 and H15 display similar strain values and humeral forces  
410 for the bow arm. However, H15 displays slightly more torsion than H10 and less than H30, while H10  
411 displays slightly more antero-posterior bending resistance than H15 and H30. The results indicate that  
412 H10 and H15 were most likely at relatively similar levels of proficiency if they engaged in archery. The  
413 lowered presence of medio-lateral bending in the models can possibly be attributed to several factors.  
414 Here, the lack of additional muscles which contribute to medio-lateral bending, the rotator cuff muscles  
415 for example, could also skew the models to display slightly greater antero-posterior strain instead. A  
416 further, relevant consideration is that of proficiency in the activity. Elite archers have been shown to  
417 display a noticeable difference with muscle usage, technique and muscle power in comparison to non-  
418 archers (Simsek, Cerrah, Ertan, & Soylu, 2019; Simsek et al., 2018), with the archery results showing  
419 similar trends in terms of strain, possibly indicating the same level of proficiency. This provides support  
420 for the notion that this elite female could have participated in warfare. Moreover, archaeological evidence  
421 indicates that the elite male in Burial 32 (H10) and the elite female in Burial 21 (H15) were shot with  
422 arrows. Both were encountered facedown, with an arrowhead fashioned from an obsidian prismatic blade

423 within the ribcage of the male (Escamilla Ojeda, 2004), and the tip of a chert arrowhead embedded in the  
424 female's scapula (Serafin et al., 2014). Further study to assess female engagement in warfare behaviors is  
425 warranted.

426  
427 In contrast to the bow arm, the data shows that the draw arm force results in primarily antero-posterior  
428 bending, with less medio-lateral bending. This is mainly due to the great flexion seen at the elbow joint,  
429 and extension at the shoulder joint (Ahmad et al., 2014; Dorshorst, 2019; Ertan et al., 2011; Reddy, 2015;  
430 Simsek et al., 2018). This is supported by the draw arm models: with the bulk of the strain being shown at  
431 the midshaft, with the highest strain values for H30 and comparatively lower values for H15 and H10.  
432 There is also some torsional strain and slight medio-lateral bending visible at the proximal end of the  
433 humeri. This is most likely due to the lateral fibers of the deltoid creating torsional force with some  
434 medio-lateral bending through abduction against the great flexion seen during the draw phase (Ertan et  
435 al., 2011; Simsek et al., 2019; Simsek et al., 2018).

436  
437 It has been hypothesized that the humerus experiences high bending forces during spear thrusting for the  
438 dominant limb (the trailing arm) (Berthaume, 2014; Churchill, Weaver, & Niewoehner, 1996; Schmitt,  
439 Churchill, & Hylander, 2003). Due to the insertion of certain muscles (e.g., anterior deltoid), however, the  
440 humerus also undergoes rotation, which would apply a torsional load to the bone. The FE models for  
441 spear thrusting show the trailing arm results in higher strain values than the forward arm in H10 and H15,  
442 but not H30. The models support the notion of humeral bending as the bulk of the strain lies at the  
443 midshaft of the trailing arm. With the forward arm, the bulk of the strain appears mainly at the midshaft  
444 and proximal shaft, with the stress extending to both the proximal and distal ends, which is indicative of a  
445 combination of bending and some humeral torsion. For the forward arm, H10 also shows slightly more  
446 resistance to antero-posterior bending than H15 and H30, with H15 showing slightly more torsional  
447 resistance than H30. Alternatively, for individuals who habitually engage in spear thrusting, the  
448 proficiency, force, frequency and manner in which the thrust is carried out could alter the forces of  
449 bending or torsion on the humerus, by extension affecting diaphysis size and shape (Auerbach & Ruff,  
450 2006; Berthaume, 2014; Ruff et al., 2006; Ruff, 2018; Schmitt et al., 2003). This is evidenced by the  
451 cross-sectional geometry data, which indicates body-mass corrected J values are high for both elite male  
452 and female (0.8-1.12), in contrast to the much lower value for the commoner female ( $J = 0.49$ ) (Table 2).  
453 Cortical (CA) and total (TA) area values follow a similar trend, being absolutely lower in the commoner  
454 female compared to the elite individuals. In addition, it should also be noted that the pectoralis major  
455 muscle would increase the torsional load on the humerus, however it was excluded from the model due to  
456 its comparatively low engagement. Further, the pectoralis major does not insert strictly in the coronal

457 plane, twisting and pulling the humerus medially with the anterior deltoid, thereby making it challenging  
458 to incorporate accurately into the FE models.

459  
460 All individuals showed the most stress with spear throwing, which seemed to grossly generate more bone  
461 diaphysis stress, extending to the humeral head, with the distal end showing comparatively smaller  
462 magnitudes of stress. All three models also show a great amount of humeral torsion, with H30 displaying  
463 the smallest amount, which is consistent with evidence that spear throwing, and overhead throwing  
464 actions more broadly, produce extreme levels of humeral torque (Sabick, Torry, Kim, & Hawkins, 2004).  
465 This is also seen in the relatively greater proportion of spiral fractures which occur during overhead  
466 throwing (Cook & Strike, 2000; Ogawa & Yoshida, 1998; Shaw & Stock, 2009a). The torsional loading  
467 seen with spear throwing creates shear stress, which starts at the centroid of the strain, extending to the  
468 proximal and distal ends: this is supported by all three loading cases for spear throwing. Since the stresses  
469 created by spear throwing are circular in nature, functional bone adaptation would dictate that it would be  
470 more efficient and beneficial to increase humeral diaphyseal shape circularly to better resist forces of  
471 torsion (Berthoume, 2014; Freeston, Ferdinands, & Rooney, 2007; Maki, 2013; Roach et al., 2013; Ruff  
472 et al., 2006; Shaw & Stock, 2009a). However, the spear thrusting model values for H10 and H15 were  
473 much lower than those for spear throwing. This is most likely because spear throwing occurs with the  
474 dominant arm, and all three humeri models were left humeri. This implies handedness and right limb bias  
475 with the individuals being tested, shown in the cross-sectional data (Table 5). Human right-limb bias is  
476 ubiquitous and consistent across a large range of populations at approximately 80% (Auerbach & Ruff,  
477 2006; Ruff & Hayes, 1983b; Stock et al., 2013), with right limb habitual loading bias aligning with the FE  
478 models. Most loading cases were of bimanual activities, primarily involving humeral bending, which  
479 would increase antero-posterior robusticity and therefore increase humeral resistance to antero-posterior  
480 bending forces, evidenced by greater values of  $I_x/I_y$  among the elite individuals (Table 2). However, with  
481 unimanual spear throwing which is enacted with the dominant arm, there is almost no torsional resistance  
482 shown in any of the models and little circular robusticity, which supports the theory of right limb bias. It  
483 is also shown that the pure torsional force displayed during spear throwing is almost double the forces in  
484 spear thrusting (Gainor, Piotrowski, Puhl, Allen, & Hagen, 1980; Maki, 2013; Schmitt et al., 2003),  
485 further supporting the wide gap between spear throwing's peak strain value compared to the rest.

486  
487 The FEA results of H10 and H15 support the hypothesis that the male humerus would exhibit lower levels  
488 of strain under simulated conditions of archery and spear use in comparison to the female humeri.  
489 However, H30 displayed the lowest spear throwing peak value, and the other strain values only loosely  
490 follow the trends of H10 and H15 presenting itself as the outlier. The H10 and H15 humeri belong to

491 male and female elite individuals, respectively, whereas H30 pertains to a commoner female, suggesting  
492 labor was divided by status as well as by sex. H30 may have spent significant periods of time engaged in  
493 food preparation activities, in particular the grinding of corn, as has been observed ethnographically and  
494 ethnohistorically in maize-based agricultural societies (Ellis, 1979; Kamp, 2002). The processing of corn  
495 is an intensive bi-manual activity involving constant flexion and extension at both shoulder and elbow  
496 joints, for extended periods of time each day (Crown, 2000; Kamp, 2002). Ogilvie and Hilton (2011)  
497 showed that females practicing this type of agriculture, which likely included H30, displayed significant  
498 differences in maximum bending and torsional strength in comparison to other females and also males  
499 (Ogilvie & Hilton, 2011), and that they also showed the least humeral asymmetry. These data are  
500 consistent with inferred use of both uni- and bimanual tools, as well as the level of female workload  
501 observed through ethnohistoric and ethnoarchaeological evidence (Bridges, 1989; Bridges, 1995; Bridges,  
502 Blitz, & Solano, 2000; Crown, 2000; Ellis, 1979; Kamp, 2002; Ogilvie & Hilton, 2011). Thus, H30 would  
503 have undergone repetitive and intensive bi-manual activities, leading to mechanical adaptation to stresses  
504 and forces, increasing resistance against bending and torsion, as well as decreasing humeral asymmetry.  
505 This is supported by all the peak values shown for H30: with H30 possessing the lowest spear throwing  
506 peak value, and having the most equidistant peak strain values, showing highly decreased humeral  
507 asymmetry, in comparison to H10 and H15.

508  
509 Maggiano et al. (2008) examined the cross-sectional properties of Maya individuals from the Classic  
510 period site of Xcambó, a site characterized by significant economic growth from a salt production site to a  
511 successful commercial port. The shift from production to administration center during its occupation is  
512 reflected in the skeletal remains of Xcambó inhabitants, with a significant decrease in femoral and  
513 humeral robusticity as well as femoral rigidity indicating a lifestyle of decreased physical stress and  
514 mobility (Maggiano et al., 2008). In contrast, the samples of this study were taken from contexts  
515 associated with warfare at the Late Postclassic regional political capital of Mayapán, and permit only  
516 preliminary comparisons due to low sample size herein. Comparing the humeral diaphyseal shape  
517 ( $I_{max}/I_{min}$ ) values between populations, the right humerus of the Postclassic elite male from Mayapán  
518 Burial 32 sampled here ( $I_{max}/I_{min} = 1.74$ ) is slightly lower, and therefore a more circular outline, than  
519 the average male right humerus from both Early and Late Classic period Xcambó ( $I_{max}/I_{min} = 1.88$ )  
520 (Maggiano et al., 2008: Table 3). The  $I_{max}/I_{min}$  values for the left (1.99) and right (2.00) humeri of  
521 postclassic elite female burial 21 are similar to the average values for left (1.93) and right (1.95) humeri  
522 of Late Classic period females reported by Maggiano et al. (2008). The commoner female sampled here  
523 ( $I_{max}/I_{min} = 1.83$ , Table 2) falls within the lower bound of the Early Classic period, suggesting a similar  
524 shape.



525  
526 We note several limitations with our FE models. Several muscles were not included (e.g., latissimus  
527 dorsi, pectoralis major), due to their low engagement (Berthaume, 2014; Dorshorst, 2019; Ertan et al.,  
528 2011; Schmitt et al., 2003; Simsek et al., 2018) in comparison to the other muscles being investigated, as  
529 well as the difficulty in implementing them into each model. Also, Newtons used for muscle loading were  
530 assumed to be the same throughout all models, disregarding potential discrepancies in muscle size. This  
531 was appropriate due to the comparative nature of this study, as well as similar body mass estimates.  
532 Another important issue with the reconstruction of activity patterns is that human movement is complex,  
533 and even for a simple movement or activity, several muscles are engaged and related motions could  
534 engage similar groups of muscles. This means that other behaviors, beyond spear use and archery, could  
535 also create similar morphological differences and hence similar strain patterns. The cumulative effect of  
536 the varied activities that these individuals engaged in during their lifetimes, as well as other intrinsic (e.g.,  
537 genetics, age, sex) and extrinsic (taphonomy) factors contribute to the complexity of recreating activity  
538 patterns in ancient populations (Maggiano et al., 2008; Meyer, Nicklisch, Held, Fritsch, & Alt, 2011;  
539 Ogilvie & Hilton, 2011; Ruff et al., 2006; Ruff, 2008; Ruff, 2018; Stirland, 1998).

540

## 541 **5. Conclusion**

542 This study aimed to understand whether the three Late Postclassic individuals' humeri being analyzed  
543 were adapted to, and therefore likely to have engaged in, activities of warfare. When the loading regimes  
544 were applied to each bone, the results mostly supported the hypothesis that the male humerus exhibited  
545 lower levels of strain in comparison to the female humeri. This trend held true for all loading regimes  
546 except for spear throwing, with H30 exhibiting a peak strain value just below that of H10. Both H10 and  
547 H15 are from elite individuals, and the notion that they engaged in warfare, or at least had proficiency in  
548 spear use and bow and arrow use is plausible and supported by the results. This has implications for the  
549 notion that females could have participated in warfare. The similarity of results between the capacity of  
550 H10 and H15 to handle loading conditions of spear use and archery offer further support for this  
551 consideration. H30 also aligned with findings from previous studies of decreased humeral asymmetry in  
552 females from maize-based farming populations. This study demonstrates the insights that FEA can  
553 provide into who participated in ancient warfare and the weaponry used.

554

## 555 **Data availability**

556 All raw data collected from cross sections are presented in the text and tables and all finite element model  
557 solutions are presented in the figures. Raw Strand7 model files, containing the humeri models and muscle  
558 beam configurations are included in supplementary files.

559

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561

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949 **Figure captions**

950 **Figure 1.** Model reference for the positions of the humerus, radius, ulna, and scapula during; The full  
951 draw phase for archery (A), the acceleration phase for spear throwing (B), and the highest level of  
952 muscle activity during a spear thrusting cycle (C).

953

954 **Figure 2.** Strain patterns during the archery bow arm load cases, showing the anterior and posterior  
955 views on the left and right, respectively, for H10 (A), H15 (B), and H30 (C). With 95% von Mises  
956 (VM) strain levels during archery bow arm load cases for all humeri (D). The hotter colors correspond  
957 to higher levels of von Mises strain. Brick strain values (center column) apply to all models to permit  
958 direct comparison.

959

960 **Figure 3.** Strain patterns during the archery draw arm load cases, showing the anterior and posterior  
961 views on the left and right, respectively, for H10 (A), H15 (B), and H30 (C). With 95% von Mises  
962 (VM) strain levels during archery bow arm load cases for all humeri (D). The hotter colors correspond  
963 to higher levels of von Mises strain. Brick strain values (center column) apply to all models to permit  
964 direct comparison.

965

966 **Figure 4.** Strain patterns during the spear throwing cases, showing the anterior and posterior views on  
967 the left and right, respectively, for H10 (A), H15 (B), and H30 (C). With 95% von Mises (VM) strain  
968 levels during archery bow arm load cases for all humeri (D). The hotter colors correspond to higher  
969 levels of von Mises strain. Brick strain values (center column) apply to all models to permit direct  
970 comparison.

971

972 **Figure 5.** Strain patterns during the spear thrusting forward arm cases, showing the anterior and  
973 posterior views on the left and right, respectively, for H10 (A), H15 (B), and H30 (C). With 95% von  
974 Mises (VM) strain levels during archery bow arm load cases for all humeri (D). The hotter colors  
975 correspond to higher levels of von Mises strain. Brick strain values (center column) apply to all  
976 models to permit direct comparison.

977

978 **Figure 6.** Strain patterns during the spear thrusting trailing arm cases, showing the anterior and  
979 posterior views on the left and right, respectively, for H10 (A), H15 (B), and H30 (C). With 95% von  
980 Mises (VM) strain levels during archery bow arm load cases for all humeri (D). The hotter colors  
981 correspond to higher levels of von Mises strain. Brick strain values (center column) apply to all  
982 models to permit direct comparison.

983

984 **Figure 7.** Peak 95% strain values of each model plotted for each bone in descending order; H10 (A),  
985 H15 (B), and H30 (C), and a comparative scatter dot plot for all loading cases and humeri (D).

1 **Tables**

2 **Table 1:** Description of Maya humeri 3D models used in the Finite Element Analysis component of this study, including the number of tetrahedral  
3 elements (Tet4) generated for each model. Body mass estimates were calculated using humeral dimensions following Ruff et al. (2020) (equation 1).

4

<b>Bone Model</b>	<b>Side</b>	<b>Sex</b>	<b>Status</b>	<b>Burial # and site</b>	<b>Period</b>	<b>Tet4 Elements</b>	<b>Body mass estimate (kg)</b>	<b>Humeral maximum length (mm)</b>	<b>Humeral head diameter (mm)</b>
<i>H10</i>	Left	Male	Elite Warrior	Mayapan Burial 32	Postclassic	276,570	61.0	310.0	43.3
<i>H15</i>	Left	Female	Elite	Mayapan Burial 21	Postclassic	202,727	53.5	279.0	39.7
<i>H30</i>	Left	Female	Commoner	Cenote Sac Uayum 190	Postclassic	226,048	56.8	298.0	41.3

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**Table 2.** Cross-sectional geometry properties extracted from the midshaft (50% length) of left (H30) and paired (H10, H11 and H14, H15) humeri of Maya individuals. Values for cortical area (CA), total area (TA), and relative percent of cross section comprised of cortical bone (%CA) were standardized by body mass. Second moments of area (J) was standardised by humeral length.

Property	Left			Right	
	H10	H15	H30	H11	H14
CA <sup>1</sup>	166.53	136.57	99.36	175.24	136.52
TA <sup>1</sup>	190.55	165.83	130.74	207.80	154.26
%CA <sup>1</sup>	0.87	0.82	0.76	0.84	0.64
J <sup>2</sup>	1.00	0.80	0.49	1.12	0.81
I <sub>x</sub>	10,964.49	7,210.53	4,568.87	13,801.37	6,158.39
I <sub>y</sub>	8,004.63	4,783.07	3,733.19	9,523.65	5,168.97
I <sub>x</sub> /I <sub>y</sub>	1.37	1.51	1.22	1.45	1.19
I <sub>max</sub>	12,203.86	7,978.09	5,368.39	14,822.18	7,550.48
I <sub>min</sub>	6,765.26	4,015.51	2,933.67	8,502.85	3,776.88
I <sub>max</sub> /I <sub>min</sub>	1.80	1.99	1.83	1.74	2.00

<sup>1</sup> Cortical areas were standardised using body mass estimates that were calculated using Ruff et al. 2020 formula.

<sup>2</sup> Second moments of area were standardised using humeral length.

**Table 3.** Muscles incorporated into Finite Element Analysis models for spear use and archery.

<b>Archery</b>	<b>Spear Use</b>
Triceps Brachii (All Heads) (Berthaume, 2014; Peterson, 1998; Rhodes & Churchill, 2009)	Triceps Brachii (Medial and Lateral Heads) (Berthaume, 2014; Peterson, 1998; Rhodes & Churchill, 2009)
Biceps Brachii (Peterson, 1998)	Infraspinatus (Maki, 2013)
Brachialis (Peterson, 1998)	Supraspinatus (Berthaume, 2014)
Deltoid (All 3 Sets Of Fibres) (Berthaume, 2014; Rhodes & Knüsel, 2005)	Deltoid (All 3 Sets of Fibres)(Berthaume, 2014; Rhodes & Knüsel, 2005)

**Table 4.** Peak Force in Newtons (N) of muscles that were incorporated into the Finite Element model for each humerus.

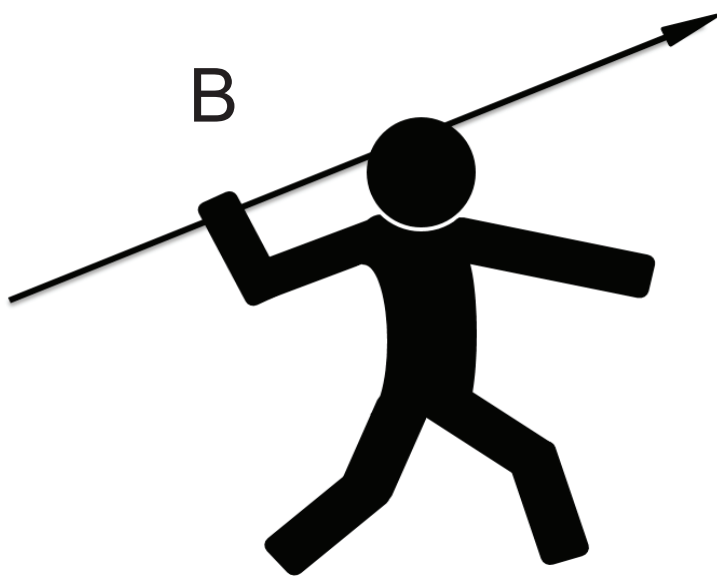
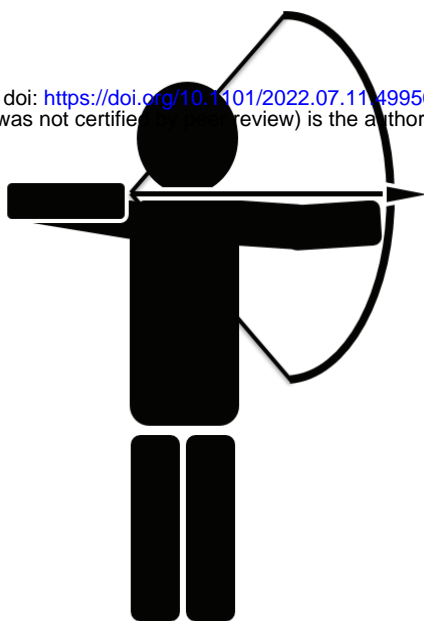
<b>Muscle</b>	<b>Peak Force (N)</b>
<i>Shoulder</i> (An et al., 1981; Garner & Pandy, 2001; Holzbaaur et al., 2005; Langenderfer et al., 2004; Lieber et al., 1992; Murray et al., 2000; Robb, 1998; Zajac, 1989)	1142.6
Deltoid	1142.6
Anterior	259.9
Middle	487.8
Posterior	1210.8
Supraspinatus	
Infraspinatus	798.5
<i>Elbow</i> (An et al., 1981; Garner & Pandy, 2001; Holzbaaur et al., 2005; Langenderfer et al., 2004; Lieber et al., 1992; Murray et al., 2000; Robb, 1998; Zajac, 1989)	624.3
Triceps	624.3
Long	624.3
Lateral	
Medial	
Biceps	
Long	
Short	
Brachialis	

**Table 5.** Comparison of asymmetry in cortical area (CA) and total area (TA) values extracted from the midshaft of paired (H10 and H11, H15 and H14) humeri, representing elite individuals from the Maya postclassic period.

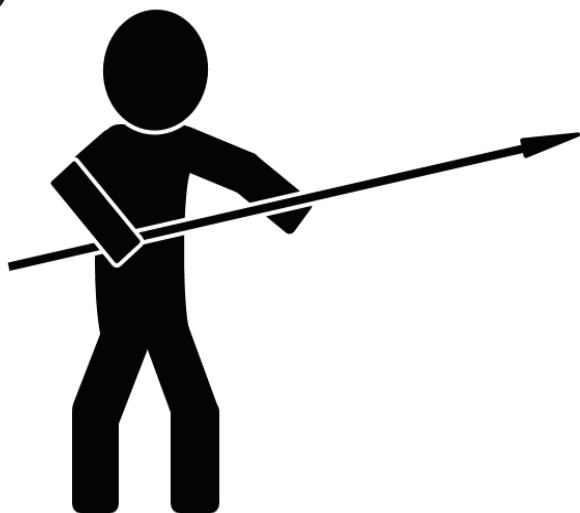
	<b>Left</b>			<b>Right</b>		
	H10	H11	Side Diff <sup>3</sup>	H15	H14	Side Diff
CA	166.53	175.24	5.23%	136.57	136.52	0.73%
TA	190.55	207.80	9.05%	165.83	154.26	7.50%

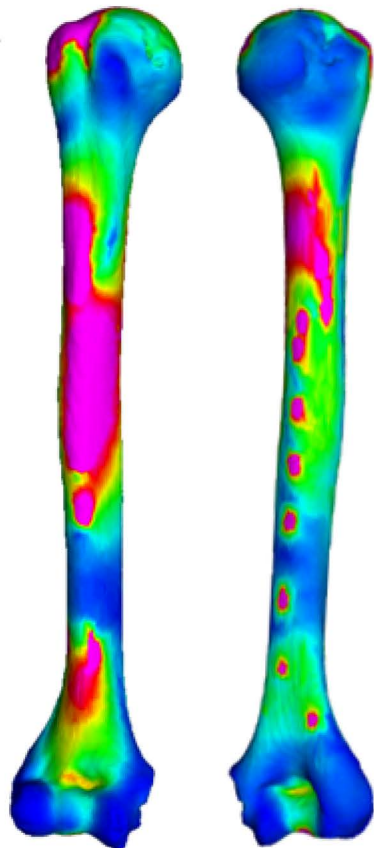
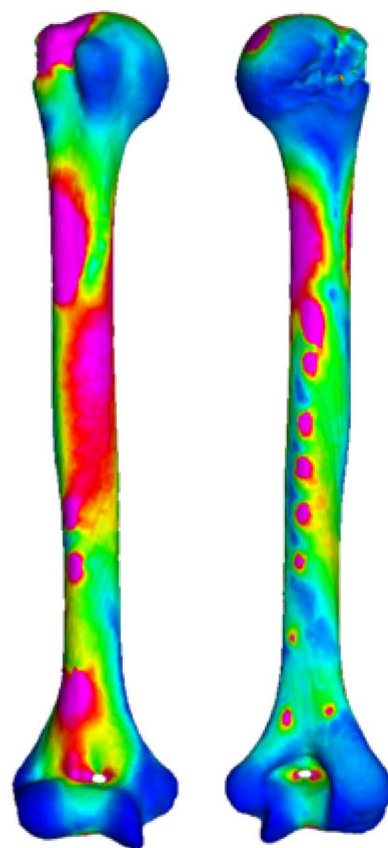
<sup>3</sup> Percentage bilateral asymmetry between left and right-side humeri =  $100 * (\text{maximum} - \text{minimum}) / \text{minimum}$ .



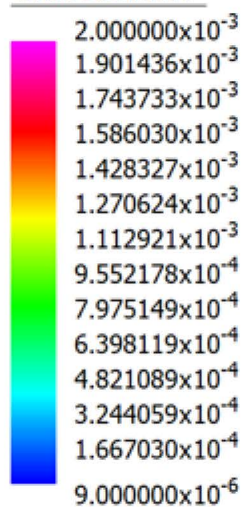
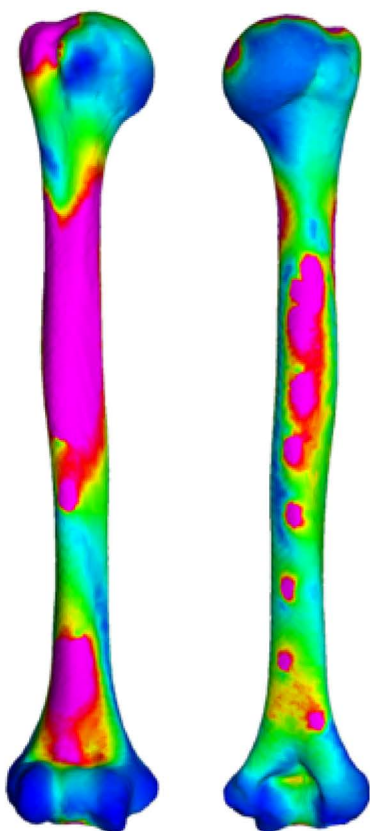


C

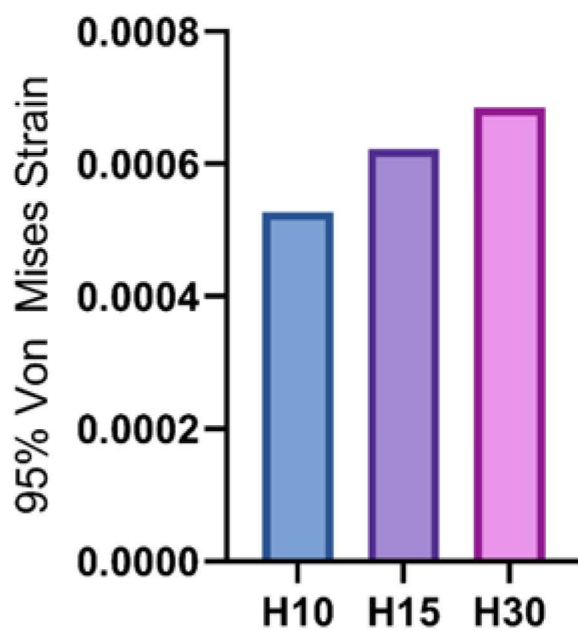


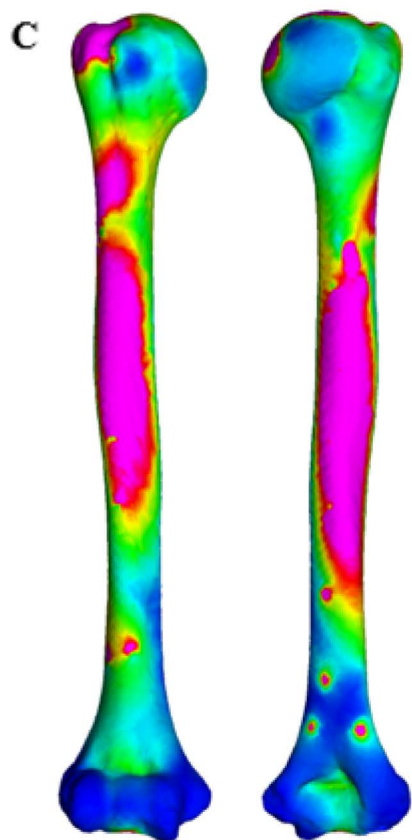
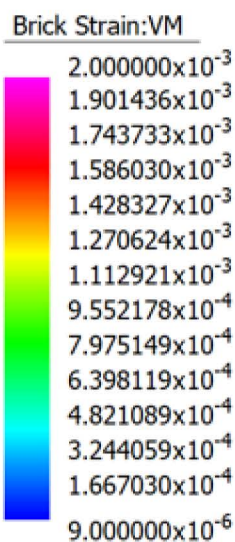
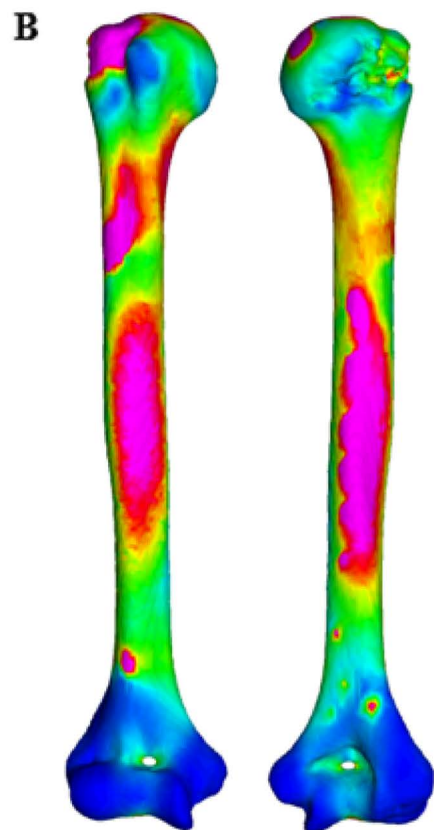
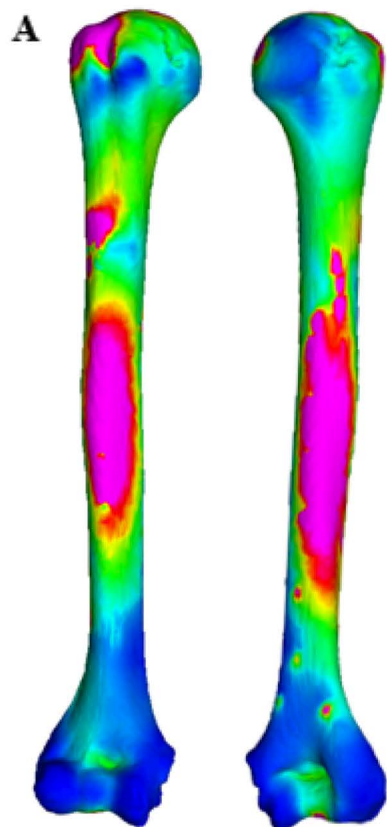
**A****B**

Brick Strain:VM

**C****D**

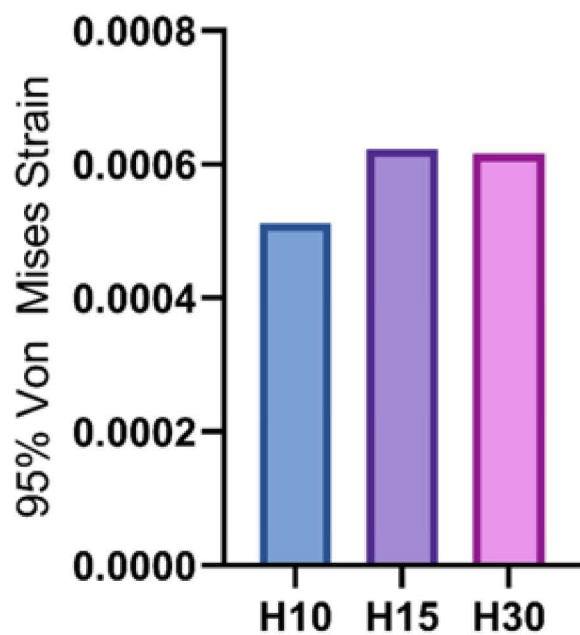
### Archery Bow Arm

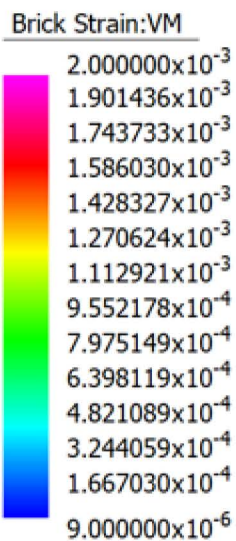
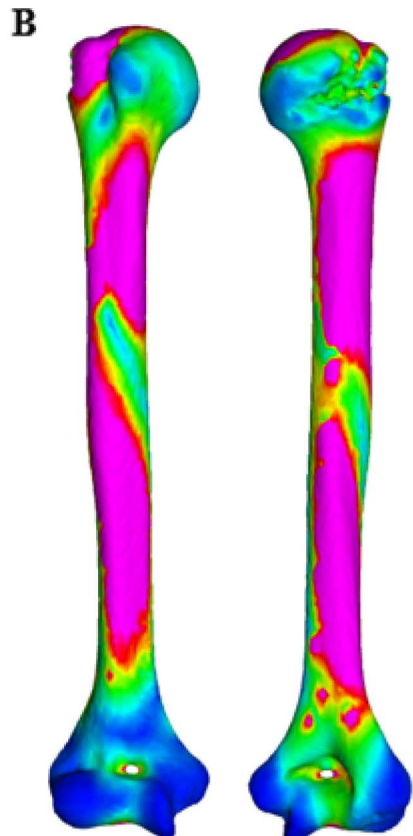
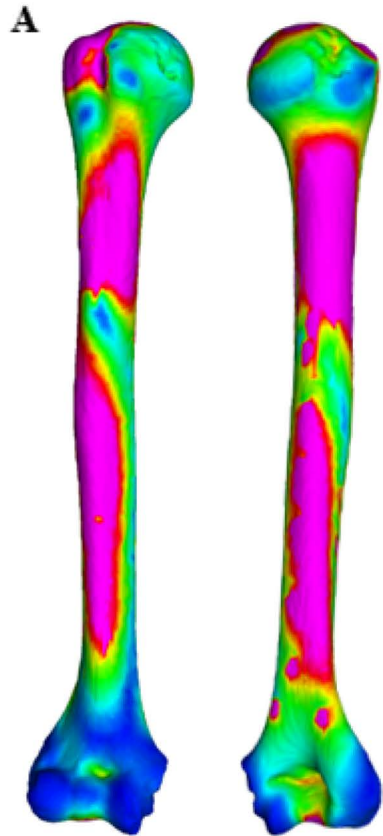




**D**

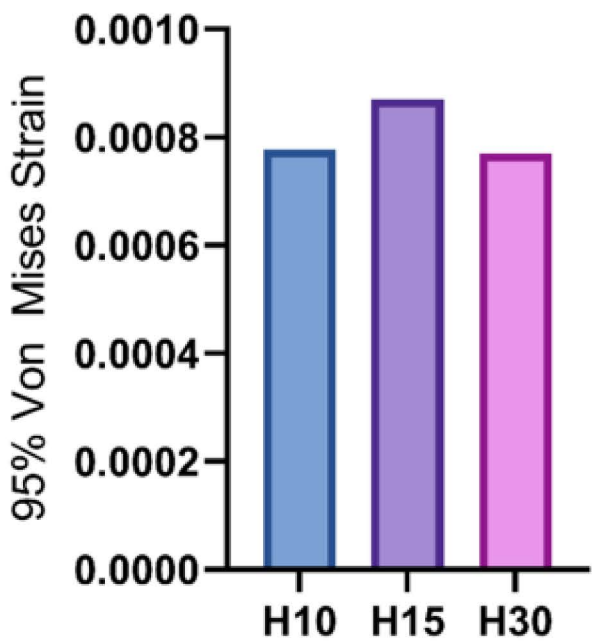
**Archery Draw Arm**

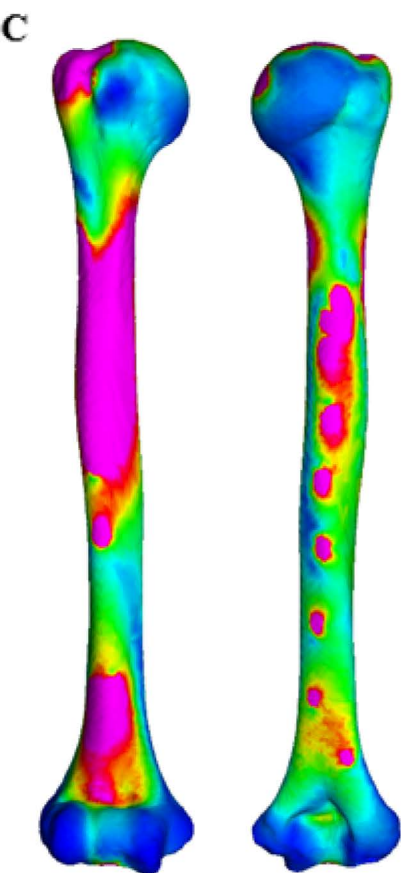
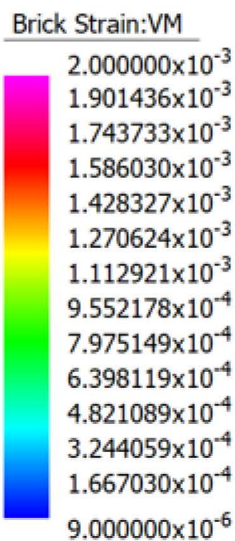
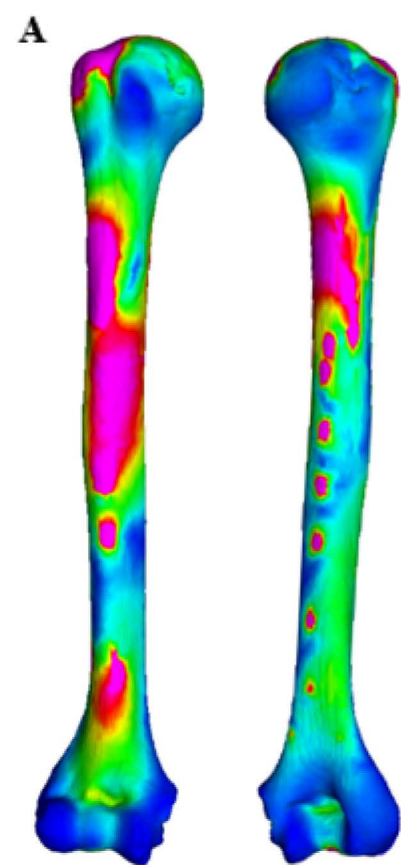




**D**

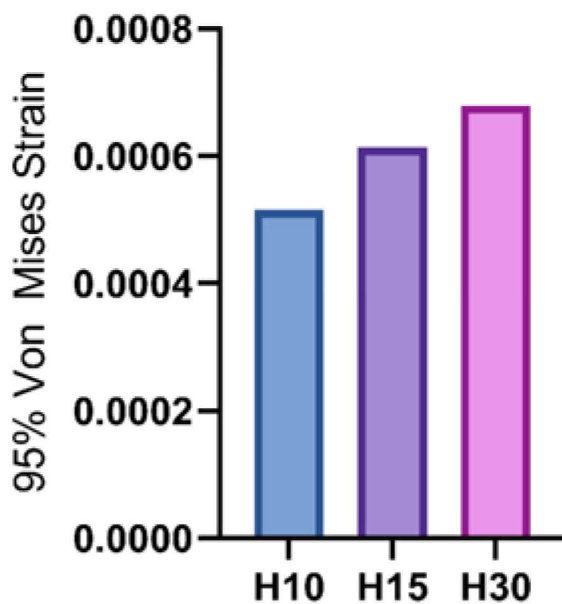
**Spear Throwing**

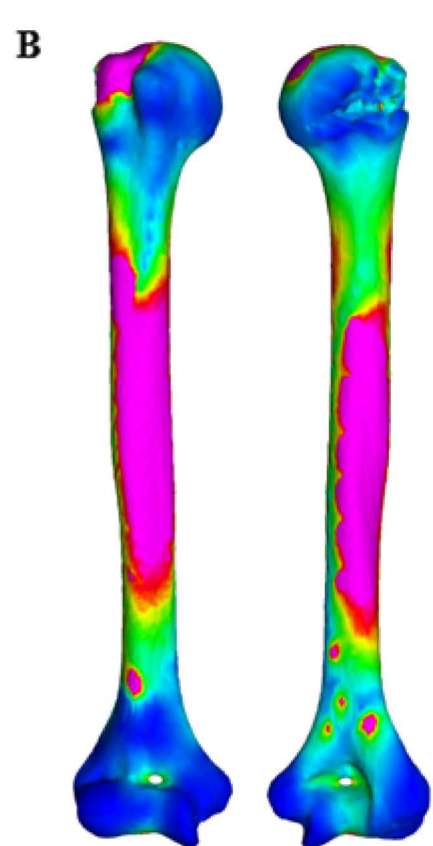
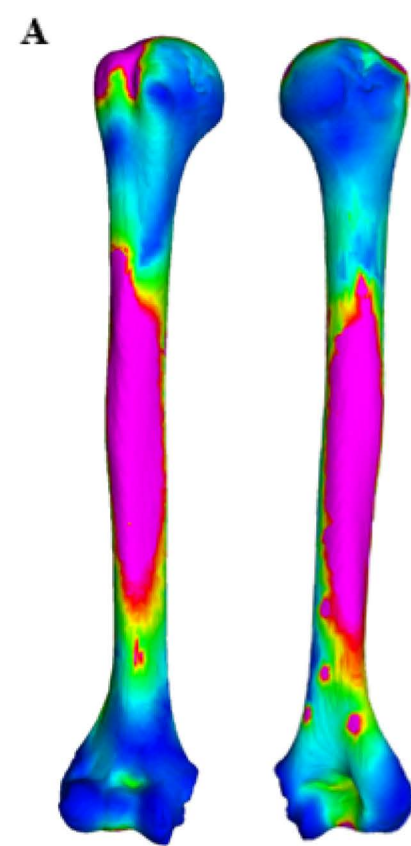




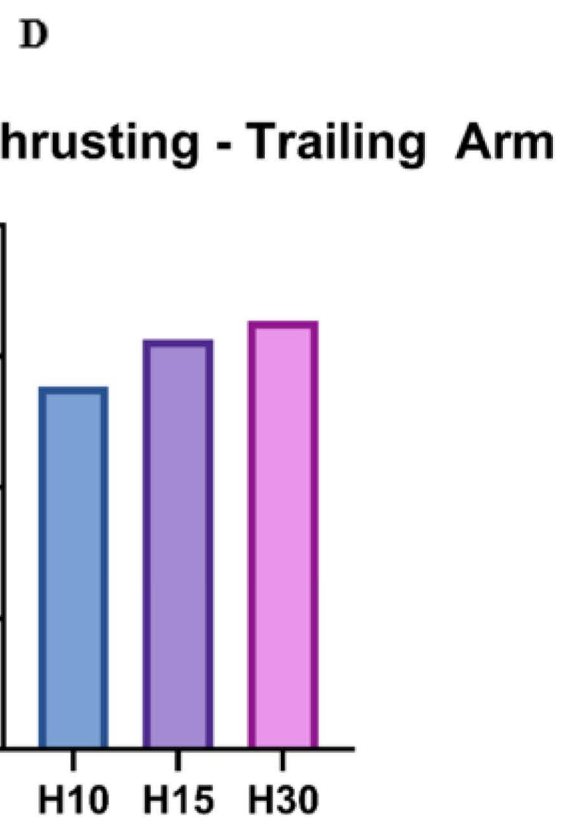
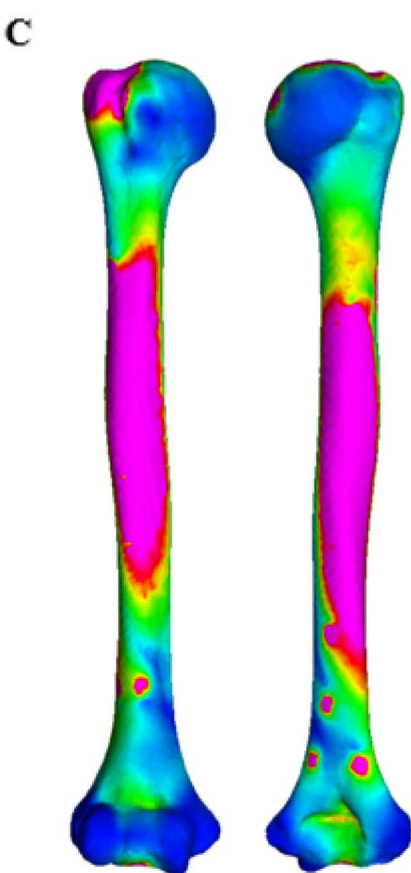
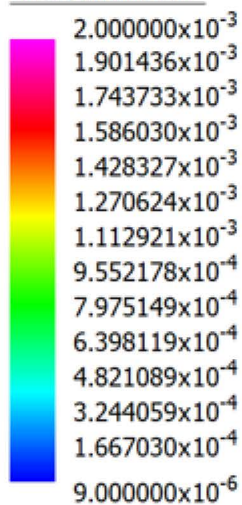
**D**

### Spear Thrusting - Forward Arm



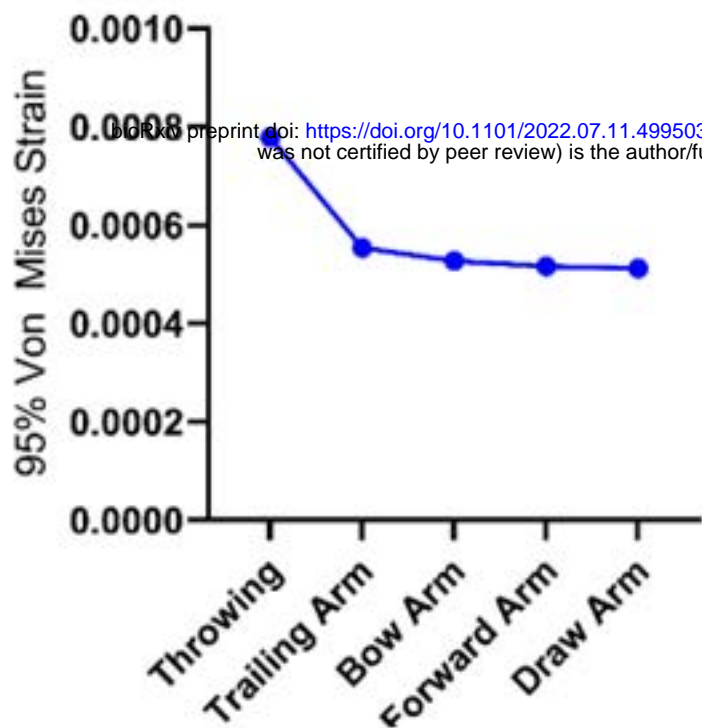


Brick Strain:VM



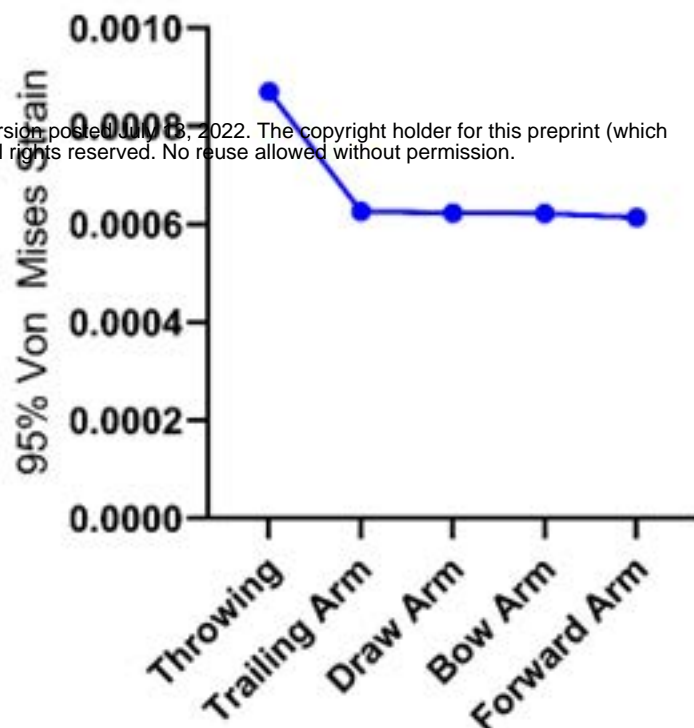
A

H10



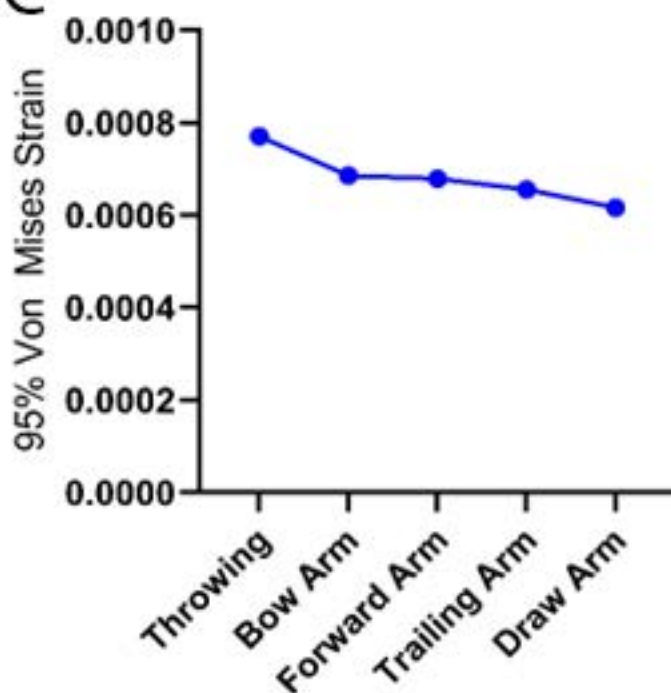
B

H15



C

H30



D

