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1 The manual pressures of stone tool behaviors and their implications for the evolution of
2 the human hand.

3

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19

20 **Key words:** Hand evolution; Force; Stone tool use; Plio-Pleistocene; Lower Paleolithic.

21

22

23 **ABSTRACT**

24 It is widely agreed that biomechanical stresses imposed by stone tool behaviors
25 influenced the evolution of the human hand. Though archaeological evidence suggests
26 that early hominins participated in a variety of tool behaviors, it is unlikely that all
27 behaviors equally influenced modern human hand anatomy. It is more probable that a
28 behavior's likelihood of exerting a selective pressure was a weighted function of the
29 magnitude of stresses associated with that behavior, the benefits received from it, and
30 the amount of time spent performing it. Based on this premise, we focused on the first
31 part of that equation and evaluated magnitudes of stresses associated with stone tool
32 behaviors thought to have been commonly practiced by early hominins, to determine
33 which placed the greatest loads on the digits. Manual pressure data were gathered from
34 39 human subjects using a Novel Pliance[®] manual pressure system while they
35 participated in multiple Plio-Pleistocene tool behaviors: nut-cracking, marrow acquisition
36 with a hammerstone, flake production with a hammerstone, and handaxe and flake use.
37 Manual pressure distributions varied significantly according to behavior, though there
38 was a tendency for regions of the hand subject to the lowest pressures (e.g., proximal
39 phalanges) to be affected less by behavior type. Hammerstone use during marrow
40 acquisition and flake production consistently placed the greatest loads on the digits
41 collectively, on each digit and on each phalanx. Our results suggest that, based solely
42 on the magnitudes of stresses, hammerstone use during marrow acquisition and flake
43 production are the most likely of the assessed behaviors to have influenced the
44 anatomical and functional evolution of the human hand.

45

46 **Introduction**

47 Stone tool behaviors are widely regarded as key innovations of the genus *Homo*
48 that arguably gave early tool-using hominins significant competitive advantages relative
49 to other organisms. They enabled early hominins to expand into new ecological and
50 dietary niches (e.g., Unger et al., 2006; Braun et al., 2010), made possible multiple
51 migration events out of Africa (e.g., Lycett and von Cramon-Taubadel, 2008),
52 contributed to the reorganization and enlargement of the brain (e.g., Stout et al., 2008;
53 McPherron et al., 2010), and influenced the evolution of the human hand and upper limb
54 anatomy (e.g., Napier, 1962; Rhodes and Churchill, 2009; Roach and Richmond, 2015).
55 In particular, Darwin (1871) was the first to propose a connection between stone tool
56 behaviors and modern human hand morphology, and the discovery of hominin hand
57 bones in association with Oldowan stone tools at Olduvai Gorge provided evidence in
58 support of this association (Napier, 1962).

59 Hominins are known to have participated in a variety of stone tool behaviors—for
60 example, nut-cracking (Goren-Inbar et al., 2002; Arroyo et al., 2016), flake production
61 (Toth, 1985; Roche et al., 1999; Sharon, 2008), animal and plant tissue processing
62 (Bunn, 1981; Domínguez-Rodrigo et al., 2001)—and these behaviors all involve
63 different materials, different end goals, and different patterns of force and motion for the
64 upper limb. Therefore, it is unlikely that each behavior exerted equal influence on the
65 evolution of the modern human hand (Key and Lycett, 2017). Instead, a behavior's
66 likelihood of exerting a selective pressure on the hand is a function of the magnitude of
67 stresses and hand/tool relationship associated with that behavior, the benefit received
68 from it, and the amount of time spent performing it (Marzke, 1997; Rolian et al., 2011;

69 Key, 2016). The last of these criteria remains difficult to estimate, but experimental
70 studies can provide some insight into the first three.

71 During manual behaviors, stone tool-related and otherwise, the internal stresses
72 occurring at joint surfaces are many times higher than those expected given the
73 external forces acting on the hand (Cooney and Chao, 1977; Chao et al., 1989). The
74 stresses occurring at any one joint surface will vary depending on a variety of factors,
75 including the joint angles, digit dimensions, internal muscle forces, and external loads
76 (Rolian et al., 2011). For example, for any given joint angle and digit dimension, the
77 internal forces at the first metacarpophalangeal joint are approximately five to six times
78 greater than the associated external force experienced at the pollical distal phalanx, and
79 those at the carpometacarpal joint are ~12 times higher (Cooney and Chao, 1977). The
80 transition from a hand marked by small joint surfaces or longer fingers relative to the
81 thumb length, as interpreted for many early australopiths (e.g., Green and Gordon,
82 2008; Lovejoy et al., 2009; but see Alba et al., 2003; Kivell et al., 2011; Almécija and
83 Alba, 2014; Kivell, 2015) to a hand with larger joint surfaces and short fingers relative to
84 a long thumb, as seen in later *Homo* (e.g., Lorenzo et al., 1999; Niewoehner, 2001; but
85 see Kivell et al., 2015), is thought to reflect adaptive changes to meet the biomechanical
86 demands of the high external forces involved in stone tool behaviors (Susman, 1994;
87 Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Skinner et al., 2015; but
88 see Weiss, 2012). The implication that high force, high stress behaviors will elicit a
89 stronger selective response rather than repetitive, low stress behaviors (such as those
90 associated with the development of osteoarthritis) is supported by evidence that the
91 manual osteological dimensions of modern humans offer biomechanical advantages

92 during hammer stone use (Rolian et al., 2011). From a bone functional adaptation
93 perspective, there appears to be a minimum strain threshold to stimulate bone
94 remodeling and modelling (Burr, 1985; Rubin and Lanyon, 1985; Frost, 1987), although
95 there is much debate regarding the effects of variation in load magnitude, frequency and
96 duration on bone form (for a review, see Bertram and Swartz, 1991; Kivell 2016). We
97 recognize that selection was also influenced by the cost/benefit ratio of a particular
98 behavior and the amount of time spent doing it (see above), and it is theoretically
99 possible that selection was responding to low stress, repetitive behaviors. However, in
100 the absence of known frequency of particular behaviors, we suggest that high force,
101 high stress behaviors would elicit a strong selective response on hand morphology
102 (Biewener, 1993; Kopperdahl and Keaveny, 1998).

103 By necessity, hypotheses citing stone tool behaviors in general as the primary
104 selective pressure acting on hominin hands imply that all varieties of such behaviors
105 impose similar biomechanical demands (e.g., manual loading patterns) and result in
106 similar joint stresses. However, multiple lines of evidence suggest that loading of the
107 hand varies substantially across different stone tool behaviors. Electromyographic
108 studies report variable muscle recruitment patterns during stone tool use and stone tool
109 manufacture behaviors, particularly in regard to the flexor pollicis longus (FPL) muscle
110 (Hamrick et al., 1998; Marzke et al., 1998), the largest and most powerful thumb flexor.
111 Furthermore, Marzke et al. (1998) found that recruitment levels of FPL varied with
112 knapping skill level just within stone tool production itself. This observed variability in
113 muscle recruitment patterns was indirectly supported by Key et al. (2017), who reported

114 that experienced tool-makers used a variety of hammerstone grip strategies during
115 knapping experiments.

116 Chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) tool use offers further
117 evidence of the unique demands imposed by various tool behaviors. Wild chimpanzees
118 are well known for their adeptness at wielding hammerstones to crack open nuts
119 (Whiten et al., 1999; Carvalho et al., 2008). Although bonobos rarely use tools in the
120 wild (Hohmann and Fruth, 2003), at least one group of bonobos in a sanctuary includes
121 adept nut-crackers who use a variety of different hammerstone grips (Neufuss et al.,
122 2017). However, captive bonobos have shown limited success in using a hammerstone
123 to produce flakes (Toth et al., 1993; Roffman et al., 2006). Together, these lines of
124 evidence suggest that hand postures, loading regimes, and, by extension,
125 biomechanical demands are distinct from one stone tool behavior to the next. To better
126 understand the potential evolutionary influences of these behaviors, it is necessary to
127 determine which of the stone tool behaviors impose the greatest loads on the human
128 hand and thus are perhaps most likely to have exerted selective pressures on the
129 evolution of modern human hand anatomy.

130 Although the variety of biomechanical strategies required to perform the suite of
131 behaviors in which early hominins engaged is not often accounted for when discussing
132 the selective pressures they applied to the human hand or human body in general (but
133 see Hamrick et al., 1998), some researchers have tested specific behaviors in isolation
134 (e.g., Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Key, 2016).
135 However, due to the lack of necessary and comparable data across all possible
136 behaviors, most researchers simply discuss the adaptive influence of ‘stone tool

137 behaviors' in general (e.g., Leakey et al., 1964; Susman, 1998; Kivell et al., 2011; Kivell,
138 2015). Neither option is entirely satisfactory; the former practice may remove the
139 behavior from the larger biomechanical context of the organism (e.g., requirements of,
140 or influences on the organism), while the latter groups together behaviors that are
141 biomechanically dissimilar, such as nut-cracking, butchering and flake production. Both
142 may mask important selective differences across behaviors, possibly leading
143 researchers to overlook or misinterpret behavioral signals implied by paleontological
144 and/or archaeological assemblages. Although it is difficult to demonstrate cause and
145 effect relationships between stone tool behaviors and anatomical adaptations,
146 understanding the biomechanical relationships between stone tools and the modern
147 human hand may allow us to make more informed hypotheses about the influence of
148 these behaviors on bony and/or soft tissue anatomy.

149 Here we investigate the pressures acting on the digits of the dominant hand
150 during various stone tool behaviors for which there is evidence of hominin participation
151 during the Plio-Pleistocene: nut-cracking, flake production, tissue-processing with flakes
152 and hand axes, and marrow acquisition with a hammerstone (e.g., Toth, 1985;
153 Blumenschine et al., 1991; Kimbel et al., 1996; de Heinzelin et al., 1999; Goren-Inbar et
154 al., 2002; Bello et al., 2009; Braun et al., 2010; Arroyo and de la Torre, 2016). Based on
155 the framework outlined above (i.e., the likelihood of selective prominence for manual
156 behaviors is a function of load magnitude, benefit, and time), we focus on the first
157 criterion, and use pressure data to evaluate which of the assessed behaviors are most
158 likely to have influenced the evolution of human digits. In regard to the influence of load
159 magnitude, we pose three questions: (1) are assessed stone tool behaviors

160 characterized by a similar digital pressure distribution pattern (e.g., is pressure always
161 highest on the third digit?); (2) which behavior(s) impose(s) the greatest overall
162 biomechanical stress; and (3) if digital pressure distributions differ across behaviors,
163 how are pressures distributed during the highest stress behaviors? Previous
164 experimental research has shown much greater kinetic energy at the time of contact
165 during human stone tool knapping (~7.37 J; Bril et al. 2010) than during nut-cracking
166 (~0.4 J for walnuts, ~0.5 J for Brazil nuts in human adults; Bril et al., 2012) and thus we
167 predict greater pressures on the digits during flake production. However, we have no
168 expectations regarding how pressures might vary across the digits or compare across
169 other behaviors tested in this study. We analyze manual pressures at three anatomical
170 levels—the digits as a group, the digits, and the phalanges—to facilitate the
171 development and evaluation of hypotheses regarding which regions of the digits are
172 most likely to reflect adaptive responses to stone tool behaviors and to increase
173 certainty that an evolutionarily important behavior is not overlooked. For example, a
174 behavior that imposes the greatest loads on the digits collectively may not have been
175 the behavior that placed the greatest loads on the thumb or the distal phalanges, both
176 regions of the hand thought to have undergone significant selection in human evolution
177 (e.g., Susman, 1988; Alba et al., 2003; Kivell et al., 2011; Almécija and Alba, 2014;
178 Kivell, 2015; but see Rolian et al., 2010).

179

180 **Methods**

181 *Participants*

182 Pressure data were recorded on the dominant hand of 39 human subjects (36
183 females and 3 males) during the performance of behaviors for which there is evidence
184 in the Plio-Pleistocene. The tested behaviors included cracking nuts with a
185 hammerstone (Goren-Inbar et al., 2002; Arroyo and de la Torre, 2016), slicing animal
186 tissue with a flake and a handaxe (Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997),
187 accessing the marrow cavity of a long bone with a hammerstone and a chopper
188 (Blumenschine, 1995; Blumenschine and Pobiner, 2007), and making Oldowan-like
189 flakes (Semaw, 2000; Braun et al., 2009; Stout et al., 2010). Participants ranged in age
190 from 18 to 35 years old and all but two (one female and one male) were right handed.
191 All subjects had no prior experience making or using stone tools. Although previous
192 work has shown substantial interindividual variation in the kinematics of the upper limb
193 during stone tool knapping within both novice and expert knappers (Rein et al., 2014),
194 we include only novice participants to help reduce two confounding effects: (1) variation
195 in skill for any given behavior among participants, and (2) variation in the skill
196 possessed by a single participant among all tested behaviors. Data were collected from
197 participants who provided informed consent under a protocol approved by the
198 Institutional Review Board of Chatham University.

199

200 *Experimental protocol*

201 A Novel Pliance[®] manual pressure sensor system (novel GmBh, Germany) was
202 used to record the pressures (i.e., normal force/area) acting at each sensor. The
203 technology used in the Novel Pliance[®] system has been repeatedly validated in the
204 Pedar[®] system, at pressures comparable to and higher than those associated with

205 knapping (McPoil et al., 1995; Putti et al., 2007; Williams et al., 2012; Price et al., 2016).
206 For example, Price et al., (2016) calibrated and validated the Pedar system for 20–600
207 kPa. The pressure-collection component of the system consists of 10 17 × 17 mm
208 sensors (digits I–IV) and two 10 × 10 mm sensors (digit V) covered in a conductive
209 woven textile. Each sensor feeds into a textile-based cable and all 12 of the cables are
210 connected to a single unit, which is then connected to the Pliance-x electronic analyzer
211 box. The analyzer box collects and transfers data to the computer. Sensors were placed
212 on the palmar surface of the digits of the dominant hand, near the center of the proximal
213 and distal phalanges of digits I, IV and V and the proximal, intermediate and distal
214 phalanges of digits II and III (12 sensors in total; Table 1). The textile composition of the
215 sensors (as opposed to a metallic wire based system as used in Williams et al., 2012)
216 allows the sensors to experience high loads while being flexible and resistant to
217 permanent bending or crimping damage.

218 The individual sensors were held in place on the palmar surfaces of each finger
219 using double-sided tape and a Velcro strap that was attached to the edge of the sensor
220 covering and wrapped around the dorsal aspect of the finger. Finger cots were placed
221 over each digit and subjects wore a fitted rayon/cotton/rubber blend glove to further
222 secure the sensors in place and to minimize the sensors' exposure to raw animal
223 tissues during the tissue-processing behaviors. After the sensors were secured to the
224 fingers, the sensor cables were positioned between adjacent digits and allowed to trail
225 across the dorsal aspect of the hand before wrapping around to the anterior wrist where
226 they were bundled together. Once bundled, the 12 cables were secured to the wrist
227 using a Velcro strap and compression tape (Fig. 1).

228 Prior to data collection, a 'mask' was created for each subject within the Pliance[®]
229 software to properly associate individual sensors with specific phalanges. Once the
230 sensors were in place and secure, and the mask had been created, the participant was
231 instructed to relax her or his hand to fully unload the sensors and the system was
232 zeroed out to remove any potential loads exerted by the attachment apparatus.

233 Participants progressed through randomized sets of stone tool behaviors: using a
234 hammerstone to make flakes from dacite, using a hammerstone to break into the
235 marrow cavity of a cow tibia, cracking open each of four types of in-shell nuts (almonds,
236 Brazil nuts, hazelnuts and macadamia nuts), and slicing tissue from a lamb shank using
237 small and medium flakes and small and large handaxes knapped from British (Suffolk)
238 flint by AK to standardized sizes (Table 2). For each behavior, a trial consisted of a
239 single instance of the behavior. For example, during marrow acquisition, one trial
240 consisted of one hammerstone strike against the tibia, and during tissue-processing,
241 one trial consisted of a single longitudinal slice along the long axis of the lamb shank. All
242 trials for a given behavior were completed before the participant proceeded to the next
243 behavior. All pressure data were recorded at 200 Hz.

244 All knapping occurred with participants seated in a wooden chair (seat height \approx
245 45 cm) and with a nodule of dacite held in place against one leg. Dacite (obtained from
246 Neolithics.com) was selected for its generally fine-grained and uniform quality, which
247 reduced the likelihood of inclusions or fractures and, in turn, made for more
248 straightforward flake reductions for the novice knappers. Because participants were all
249 novice knappers and to help avoid injury, each knapping session began with brief
250 instructions on both flake removal and injury prevention. This was followed by a 10 min

251 practice session, then data collection. Participants had the option of placing up to three
252 leather pads (5 mm thick each) on their legs for protection. Each participant selected
253 her or his hammerstone of choice from a selection of 10 hammerstones (< 1 kg each)
254 and were free to switch hammerstones as desired. Tool production data were collected
255 from 23 participants. Each performed 20 total trials and data analyses included those
256 trials resulting in the production of flakes as well as those that failed to produce a flake.
257 All tool use behaviors were conducted with novice participants seated on the ground in
258 their preferred sitting position (the majority chose to sit either cross-legged or kneeling
259 on both of their legs). During nut-cracking, participants were instructed to strike with
260 sufficient force to break through the shell, but to refrain from smashing the internal nut.
261 The four nut varieties were selected because their shells span a wide range of
262 toughness values, as is true of the shells of nuts consumed by extant wild primates
263 (Jennings and MacMillan, 1986; Lucas, 2004; Lucas et al., 2011). Toughness is the
264 primary material property governing critical load to failure (Chai and Lawn, 2007a,
265 2007b), and as such will have a large influence on the strategies used when cracking
266 the shells of different nut species. Nuts were inspected for shell integrity prior to testing
267 and those with cracks or other signs of failure in the shells were discarded. All nut-
268 cracking took place with the nut situated on a thick wooden cutting board (i.e., the anvil).
269 Participants typically either held the nut in place on the anvil using the first and second
270 digits of their non-dominant hand, or stabilized the nut alone on the anvil without further
271 support from their non-dominant hand. They were allowed to select the hammerstone of
272 their choice and to switch hammerstones as frequently as desired. Nut-cracking data
273 were collected and included in the analyses from all 39 participants. Each participant

274 cracked open or attempted to crack open 10 of each nut type. Nuts were discarded after
275 being struck once, regardless of whether their shell was cracked open or not.

276 Marrow acquisition and tissue-processing took place on top of a cutting board
277 placed on the ground. A cow tibia was selected for marrow acquisition because animals
278 of a similar size (class 3; Brain, 1981), are commonly found in assemblages of fauna
279 and stone tools, assumed to have been compiled by hominins (e.g., Klein, 1976; Clark
280 and Plug, 2008). During the marrow acquisition phase, participants were instructed to
281 attempt to access the marrow cavity but to refrain from exerting their maximum force to
282 prevent injury, and to concentrate their strikes on the shaft of the bone rather than the
283 epiphyses. Marrow acquisition data were collected and included in the analyses from all
284 39 participants. Each participant performed 20 trials (i.e., strikes) using the
285 hammerstone of their choice and they were allowed to switch hammerstones as
286 desired.

287 During the tissue-processing phase, the slicing protocol was the same for all
288 tools: participants sliced the shank along the long axis in an uninterrupted stroke,
289 constituting a single trial. Participants were instructed to refrain from using sawing
290 motions and from starting and stopping during a single trial. Although this protocol
291 differs from real butchery processes, the constraints were necessary to standardize the
292 behavior thereby increasing the likelihood of recording data on the same experience
293 (see limitations in the Discussion section). Tissue-processing data were collected from
294 all 39 participants, but data from two were excluded due to a recording error. Each
295 participant performed 10 trials (i.e., slices) each using four different tools: a small flake
296 (mean length = 29.2 mm), a medium sized flake (mean length = 58.3 mm), a small

297 handaxe (mean length = 119.7 mm) and a large handaxe (mean length = 168.4 mm).
298 Participants were each given a tool with a fresh cutting edge (i.e., either the other side
299 of a previously used tool or a tool with two fresh edges) and were required to use the
300 same tool for all 10 trials.

301

302 *Data analysis*

303 Pressure data were extracted, formatted, and analyzed using a series of custom
304 scripts written in the R programming language and environment (R Core Team, 2017).
305 Each sensor collected pressure data (kPa) continuously throughout each trial at 200 Hz,
306 resulting in hundreds of data points per sensor per trial. Therefore, the analyses
307 presented here are concerned with peak pressures, which were defined in three
308 different ways. First, we evaluated peak pressures in a sensor-by-sensor fashion. In
309 these cases, peak pressures were the maximum recorded pressure on each individual
310 sensor, within each trial. Second, we focused on digit-by-digit peak pressures. In these
311 cases, peak pressure for each digit during each trial was calculated by summing the
312 peak normal forces experienced by each sensor on a given digit, and then dividing by
313 the total sensor area across that digit. Third, we evaluated cumulative pressures across
314 all of the digits. Similar to the procedures used for digital analyses, within every trial
315 peak normal force measurements across all sensors were summed and then divided by
316 total sensor area.

317 Our analyses had to accommodate the fact that repeated measurements were
318 taken of each subject performing each behavior. To account for this bias, we calculated
319 the average peak pressures per sensor, per activity, per subject. In doing so, we

320 eliminated within-subject and within-activity variation. Although this ultimately reduced
321 the size of our data set, and meant that we were not explicitly examining within-subject
322 variability, we felt that such an approach was justified in the context of the current study.
323 Given that subject participants were not experienced in stone tool behaviors, central
324 tendencies of their pressure distributions are arguably more applicable for
325 understanding the general patterns by which subjects used their hands. Further, by
326 simplifying the variance structures of the data set and subsequent model fits, the results
327 are more directly interpretable.

328 To address our first question of whether the different stone tool behaviors were
329 characterized by similar distributions of pressure across the digits and how they
330 differed, peak pressures from individual sensors were used. The peak pressures
331 observed during each activity by each subject were adjusted because different subjects
332 experienced different absolute magnitudes of pressures, and we were interested in
333 analyzing consistency in distribution patterns. For each subject's average peak pressure
334 distribution during each activity (i.e., for each subject-activity pair), the pressures
335 experienced across the sensors were normalized to a scale of 0 to 1, according to the
336 following formula:

$$P_{\text{normalized}} = \frac{(P_{\text{observed}} - P_{\text{min}})}{(P_{\text{max}} - P_{\text{min}})}$$

337 Multivariate analysis of variance (MANOVA) was then used to determine the overall
338 effect of behavior type on a multivariate response that included normalized peak
339 pressures for each sensor, for each subject-activity pair.

340 Multiple steps were used to address our second question of which behaviors
341 might impose the greatest biomechanical stress upon all of the digits. First, cumulative

342 pressures across the digits were examined to identify which stone tool behaviors were
343 associated with the highest magnitude pressure measurements. Analysis of variance
344 (ANOVA), with post-hoc Tukey's honest significant difference (HSD) tests, was used to
345 compare cumulative pressures across all behaviors. Following the ANOVA results that
346 suggested there was high interindividual variation in pressure data, a linear mixed
347 effects model was fit to the data to further investigate pressure variation across
348 behaviors while accounting for subject identity as a random effect on cumulative
349 pressure.

350 Next, to address our third question, more fine-scaled analyses were conducted to
351 better understand the biomechanical differences across stone tool behaviors. MANOVA
352 was used to determine the effect of behavior type on the raw magnitudes of (1)
353 cumulative peak pressures on each digit and (2) peak pressures on each individual
354 sensor. These analyses are pertinent to developing and evaluating hypotheses
355 regarding which locations within the hand are likely to reflect anatomical adaptations to
356 the biomechanics associated with stone tool behaviors and for evaluating which stone
357 tool behaviors are the most likely to have exerted the strongest selective pressures on
358 the anatomy of the human digits.

359

360 **Results**

361 *Are different stone tool behaviors characterized by similar distributions of manual*
362 *pressure?*

363 Mean normalized peak pressure from each sensor across all participants for
364 each activity is depicted in a heat map in Figure 2. Participants did not conform to a

365 single pressure distribution pattern while performing the different stone tool behaviors
366 investigated here; instead, behavior type had a significant effect on the multivariate
367 overall pressure distribution (Pillai's Trace = 0.967, $p < 0.001$). A series of separate
368 MANOVA analyses showed that behavior's effect was not uniform; a strong significant
369 effect was observed during the various tissue-processing behaviors (Pillai's Trace =
370 0.949, $p < 0.001$), whereas all four nut-cracking behaviors resulted in statistically similar
371 distributions (Pillai's Trace = 0.197, $p = 0.771$). This similarity did not, however,
372 characterize percussive behaviors in general; a MANOVA analysis comparing pressure
373 distributions during nut-cracking behaviors as well as marrow acquisition and flake
374 production showed a strong significant behavioral effect (Pillai's Trace = 0.426, $p =$
375 0.006). This result was driven by variation in pressures on the second, fourth and fifth
376 digits and no significant effects were present along the phalanges of the thumb and third
377 digit.

378 Despite the overall differences, some consistencies in the normalized pressure
379 distributions were present. Within each digit there was a tendency for the magnitude of
380 the effect of behavior to correlate with the absolute magnitude of the load: behavior had
381 a greater effect on those regions of the digit incurring the highest relative loads (typically
382 the distal phalanges) and a lesser effect on the regions incurring the lowest relative
383 loads (typically the proximal phalanges; Table 3, Fig. 2). The thumb was the exception
384 to this pattern, being consistently relatively highly loaded regardless of the behavior.
385 The results of the MANOVA analysis of percussive pressures support this hypothesis.

386

387 *Which behaviors impose the greatest magnitude of manual pressure?*

388 Analyses to determine which behavior(s) might impose the greatest
389 biomechanical stress across the digits were conducted at multiple anatomical levels: the
390 digits as a group, the individual digits, and the individual phalanges. Results were
391 consistent across all three analytical levels: marrow acquisition and flake production
392 consistently placed the greatest loads on all of the digits as a group (Fig. 3,
393 Supplementary Online Material [SOM] Table S1), on individual digits (Fig. 4, SOM Table
394 S2), and on the phalanges (Fig. 5, SOM Table S3).

395 Behavior had a highly significant effect on the cumulative raw pressures acting
396 on the digits as a group ($p < 0.001$; Fig. 3). Post hoc pairwise comparisons showed that
397 the use of hammerstones during flake production and marrow acquisition placed
398 similarly ($p = 0.999$) high cumulative loads on the digits as a group, and both behaviors
399 imposed significantly greater pressures than all other behaviors ($p \leq 0.05$), with two
400 exceptions: pressures experienced while using a medium flake or large handaxe to slice
401 tissue, which were not statistically different from pressures experienced during flake
402 production ($p = 0.283$ and $p = 0.185$, respectively; Fig. 3). In addition, pressures
403 experienced by the digits as a group while cracking hazelnuts were significantly smaller
404 than those derived from medium flake or large handaxe use to slice tissue. All other
405 post hoc pairwise comparisons of pressures acting on the digits as a group were not
406 significantly different across the different behaviors.

407 The MANOVA results showed high variance within activities (Fig. 3), hinting at
408 potentially high inter individual variation. To examine variation across activities in a
409 more complete manner, a linear mixed effects model was fit to the data with total
410 cumulative pressure as the response, behavior type as a fixed effect and subject

411 identity as a random effect. This analysis could then include peak pressures from each
412 trial for each subject rather than the average distributions per activity. The overall mean
413 pressure for almond cracking was arbitrarily set as the reference behavior (intercept) of
414 the mixed effects model and all other behaviors were contrasted with it. Cracking Brazil
415 nuts did not involve significantly different pressures compared with almond cracking,
416 cracking hazelnuts involved significantly lower pressures, and all other behaviors were
417 associated with significantly higher total cumulative pressures (Table 4). Post hoc
418 contrasts of all pairs of behaviors, with Holm-Bonferroni corrected p-values, showed that
419 pressures imposed on the digits from cracking almonds, Brazil nuts and hazelnuts were
420 significantly lower than pressures experienced during all other behaviors ($p < 0.001$).
421 Pressures while cracking macadamia nuts were significantly greater than those while
422 cracking any other variety of nut ($p < 0.001$). They were also greater than pressures
423 experienced while using a small flake ($p < 0.001$) and similar to those while using a
424 small handaxe ($p = 0.965$) but significantly lower than the pressures experienced during
425 all other activities ($p < 0.001$).

426 When looking across the individual digits (i.e., accumulating data from sensors
427 on the same digit), behavior also had a significant effect on pressure distribution (Pillai's
428 Trace = 0.667, $p < 0.001$; Fig. 4). The strength of behavior's effect was greatest on the
429 fourth digit, followed by the first, second, third and fifth digits (Table 5). Raw pressures
430 tended to be higher on the radial side of the hand (i.e., digits I, II and III) relative to the
431 ulnar side (i.e., digits IV and V) across all behaviors (SOM Table S2), meaning that the
432 strength of the effect of behavior did not correlate with raw pressure, as was the case
433 for normalized pressures.

434 Pressures while cracking almonds, Brazil nuts and hazelnuts again clustered
435 together at the lowest end of the pressure range for the radial digits (though pressures
436 tended to differ significantly only from marrow acquisition and flake production).
437 However, on the ulnar side of the hand, these pressures were more similar to the
438 pressures experienced during tissue processing behaviors. This was driven by a
439 decrease in pressure on the fourth and fifth digits during tissue-processing behaviors
440 rather than any substantial pressure increase on the same digits during nut-cracking.
441 The comparatively low pressures on the fourth and fifth across nut-cracking and tissue-
442 processing behaviors likely reflects the rarity with which these digits were in firm contact
443 with the tool.

444 Post hoc Tukey HSD tests showed that among digits I through IV, hammerstone
445 use during flake production and marrow acquisition exerted significantly greater
446 pressures than all nut-cracking behaviors (minimum $p < 0.001$, maximum $p = 0.011$),
447 apart from pressures experienced while cracking macadamia nuts compared with flake
448 production ($p = 0.143$). Marrow acquisition and flake production also tended to impose
449 significantly greater loads on digits I, III and IV than during tissue-processing behaviors
450 (Fig. 4). The consistently high loads on the second digit across all behaviors reflected
451 participants' tendency to grasp the flakes and handaxes primarily between their first and
452 second or first, second and third digits, reserving the fourth and fifth to help steady the
453 tool or not using them at all. Pressures were always lowest on digit V across all
454 behaviors (20.69–75.83 kPa; SOM Table S2), with few statistical differences among the
455 behaviors.

456 Behavior had a significant effect on pressure at the interphalangeal level, as it did
457 at the other levels of analysis (Pillai's Trace = 1.134, $p < 0.001$). Similar to the
458 distribution pattern of normalized pressures, the strength of behavior's effect was
459 greater on those regions subject to higher loads (i.e., the distal phalanges; Table 6).
460 Marrow acquisition consistently imposed greater loads on each phalanx compared with
461 all other behaviors. This difference was significant across all phalangeal regions, apart
462 from those of the fifth digit, compared with cracking almonds, Brazil nuts and hazelnuts.
463 With few exceptions, flake production also exerted greater loads on each phalanx
464 compared to all other behavior, however a consistent pattern regarding statistical
465 significance was not present.

466

467 **Discussion**

468 Here we investigated manual pressure during Plio-Pleistocene stone tool
469 behaviors to determine which behavior(s) exposed the digits of the dominant hand to
470 the greatest magnitude of loads and thus were more likely to have influenced the
471 evolution of human digit morphology. We addressed three questions: Are different stone
472 tool behaviors characterized by similar distributions of manual pressure? Which
473 behaviors impose the greatest magnitude of digital pressure? And, finally, what patterns
474 of pressure distribution characterize the highest stress stone tool behaviors? In regard
475 to the first question, we found that participants did not conform to a single pressure
476 distribution pattern across all behaviors. In contrast, we found pressure experienced by
477 the digits collectively and by the individual digits and phalanges varied significantly
478 across the different Plio-Pleistocene tool behaviors.

479 Our finding that pressures experienced by the digits varied across the tested
480 stone tool behaviors (Fig. 2) is, on one level, to be expected and indeed, our prediction
481 that manual pressures would be lower during nut-cracking compared with flake
482 production was supported. Subjects used tools of a wide range of sizes and shapes,
483 including small flakes averaging 29.2–58.3 mm (Table 2) and hammerstones weighing
484 0.23 to ~1 kg, they had to utilize different kinematic approaches for various tasks (e.g.,
485 full arm swing versus more constrained extension at the wrist), and different magnitudes
486 of force were required to successfully accomplish each behavior. Marzke and
487 Shackley's (1986) discussion of the upper limb movements and grips used during
488 various stone tool behaviors nicely contextualizes this result. Their participants
489 exclusively used a grip known as a 'three jaw chuck' during Oldowan tool production
490 and nut-cracking with small hammerstones, which relies on the first three digits of the
491 dominant hand to grip the hammerstone. In contrast, while cutting with a small flake, the
492 tool was grasped between the pollical distal phalanx and the lateral side of the second
493 digit (Marzke and Shackley, 1986). Clearly, these postural and kinematics differences
494 are likely to result in variations in manual pressure distributions.

495 Our results, however, suggest that such factors alone are insufficient to account
496 for the observed variation, as illustrated by the differences in relative pressure
497 distributions among percussive behaviors: despite participants using the same selection
498 of hammerstones and gross similarities in the motions, behavior had a significant effect
499 on the distribution of relative pressures in comparisons of nut-cracking, marrow
500 acquisition and flake production (Pillai's Trace = 0.426, $p = 0.006$; Figs. 4 and 5). This
501 was in sharp contrast to the strong statistical similarity among nut-cracking behaviors

502 alone (Pillai's Trace = 0.197, $p < 0.771$). These results suggest that the force needed to
503 carry out a behavior—in these cases, load to failure of the bone, stone or nut—also
504 influences the hand-tool pressure relationship and resulting distribution of relative
505 pressures. It appears that during activities such as nut-cracking, when relatively low
506 forces are required to cause material failure, a generic hand-tool posture that is not
507 specialized to a specific high-loading condition can be used, resulting in a similar
508 distribution of relative pressures across nut-cracking behaviors. However, more forceful
509 activities, such as marrow acquisition and flake production, require specialization to
510 maintain precise control of the hammerstone and to deliver the requisite forces while
511 also avoiding injury.

512 This proposal is supported by the strong tendency for the strength of behavior's
513 effect to correlate positively with the relative magnitude of the load at a given sensor
514 across all behaviors (Table 3). Thus, there was more variability in the relative pressures
515 acting on the distal phalanges, which always experience the highest peak pressures,
516 compared with the proximal phalanges and (generally) the intermediate phalanges. This
517 pattern suggests that, regardless of which tool was being used, participants tended to
518 stabilize the tool primarily with the distal phalanges and then adjusted the amount of
519 force they applied at these phalanges according to the task at hand. Simultaneously,
520 they tended to use the intermediate and proximal regions of the digits on a more limited
521 basis, and at consistently low pressures. We found strong variability in relative
522 pressures acting on the fourth and fifth distal phalanges in particular, which likely
523 reflects the widely variable roles that these digital regions played across the various tool
524 behaviors, as described above. At one extreme, these digits were consistently used and

525 subject to the highest intra-digit pressures during nut-cracking, and at the other they
526 were inconsistently used with the lowest inter sensor loads recorded during slicing with
527 smaller cutting tools (Fig. 5).

528 The thumb was the exception to this pattern: despite the fact that loads on the
529 pollical distal phalanx were significantly greater than those on the pollical proximal
530 phalanx, behavior had a rather small effect on the relative loads acting on the distal
531 phalanx, and a far stronger effect on the proximal phalanx (Table 3). In other words, the
532 pollical distal phalanx tended to be subjected to the same relative loads (i.e., the
533 greatest relative load), irrespective of behavior (Fig. 2). This illustrates the consistency
534 in how the thumb was used: regardless of how the hand was oriented relative to the
535 tool, the thumb acted as the stabilizing fulcrum or clamp against the tool or the other
536 digits (Napier, 1956; Marzke, 1997). These results contrast with those of Key (2016),
537 who found that stone carrying behaviors did not consistently result in heavy loading on
538 the thumb, further emphasizing the important role of this digit during specific forceful
539 stone tool use activities (such as those examined here). In regard to knapping, this is
540 similar to results reported by Rolian et al. (2011), and in contrast to those reported by
541 Williams et al. (2012), who reported that loads were highest on the second and third
542 digits compared with the thumb. As suggested by Key and Dunmore (2015), the
543 difference in these findings may reflect simple diversity in preferred hand postures
544 during knapping, or it may be a result of the composition of the participant pools: novice
545 tool makers were studied here and by Rolian et al. (2011), whereas Williams et al.
546 (2012) studied only experienced tool makers.

547 Upon demonstrating that stone tool behaviors are not characterized by a single
548 pressure distribution pattern, we examined the absolute loads to establish which
549 behaviors placed the greatest biomechanical stress on the digits collectively and, by
550 extension, may be more likely to have imposed a selective pressure on the digits. We
551 first demonstrated that, at each anatomical level of analysis, behavior had a significant
552 effect on absolute pressure magnitudes—cumulative pressures acting across the digits
553 as a group ($p < 0.001$; Fig. 3), the individual digits (Pillai's Trace = 0.667, $p < 0.001$; Fig.
554 4), and the individual phalanges (Pillai's Trace = 1.134, $p < 0.001$; Fig. 5). Thus, both
555 the relative pressures (i.e., normalized data) and the absolute pressures (i.e., raw data)
556 acting at a given location are influenced by the behavior being performed, together
557 strongly indicating that some behaviors may be more suitable candidates for those
558 imposing selective pressures on the digits than others.

559 The two most striking results of the analyses of the absolute pressures imposed
560 by the tool behaviors were (1) the clear distinction in the high pressures incurred by
561 hammerstone use during marrow acquisition and flake production relative to all other
562 assessed behaviors, and (2) the further distinction of low pressures during nut-cracking
563 compared with all other behaviors. Our results revealed that relative to all other
564 assessed behaviors, hammerstone use during marrow acquisition and flake production
565 resulted in significantly higher pressures experienced by the digits as a group (Fig. 3).
566 Similarly, marrow acquisition and flake production also imposed significantly greater
567 loads on the radial four digits relative to nut-cracking behaviors (other than loads on
568 digit II while cracking macadamia nuts compared with flake production). With the
569 exception of loads acting on the second digit, marrow acquisition and flake production

570 also tended to impose significantly greater loads on the digits compared with tissue
571 processing behaviors. A similar pattern, although not always statistically significant, was
572 found at the inter phalangeal level, such that peak pressures were generally highest
573 during marrow acquisition and flake production, especially on the distal phalanges,
574 compared to all other behaviors (Fig. 5).

575 On the radial four digits, hammerstone use during marrow acquisition and flake
576 production consistently imposed significantly greater loads compared with the other
577 tested behaviors on the distal phalanges. This was not consistently the case regarding
578 the intermediate and proximal phalanges. Loads experienced at the distal phalanges
579 have a larger contribution toward resultant joint stresses than do those experienced at
580 the more proximal regions of the rays (Cooney and Chao, 1977). Thus, it is reasonable
581 to argue that behaviors that concentrated loads on the distal phalanges would have
582 been more influential from an evolutionary standpoint than those that concentrated
583 loads on the intermediate and/or proximal regions.

584 In contrast to marrow acquisition and flake production, pressures experienced
585 during nut-cracking behaviors, particularly when cracking almonds, Brazil nuts and
586 hazelnuts, were generally far lower than pressures incurred during all other behaviors.
587 This pattern was found in both pressures experienced by the digits as a group, where
588 the differences were statistically significant, and among the three radial digits.
589 Macadamia nuts were the exception to this pattern, such that pressures incurred by the
590 digits as a group or by the individual digits were generally higher than other nut-cracking
591 behaviors and most similar to pressures experienced during tissue-processing
592 behaviors. The difficulty participants consistently had in cracking them resulted not from

593 shell toughness but rather from their tendency to roll away when struck, due to their
594 smooth, round shells. Thus, the higher loads seen while cracking macadamia nuts more
595 likely reflect participants' use of high-force strikes in an attempt to prevent the nut from
596 rolling away rather than what was needed to induce shell failure. Additionally,
597 participants' lack of familiarity with nut-cracking behaviors likely also impacted their
598 performance (Brill et al., 2010, 2012), both in regard to pressures experienced and their
599 ability to successfully rupture the shell (see below).

600

601 *Implications for the evolution of the human digits and hand*

602 It is generally assumed that the modern human hand morphology is, at least in
603 part, a byproduct of stone tool-related behaviors, and particularly a commitment to
604 intensified use of these behaviors (e.g., Washburn, 1960; Napier, 1962; Marzke, 1997;
605 Tocheri et al. 2008). Paleoanthropologists have reasoned that behaviors that involve
606 higher load magnitudes or stronger muscle recruitment patterns, and which conferred a
607 substantial benefit on the actor, such as the acquisition of high quality food items, were
608 more likely to exert selective pressures on the evolution of human hand anatomy (e.g.,
609 Susman, 1994; Hamrick et al., 1998; Marzke et al., 1998; Rolian et al., 2011; Williams et
610 al., 2012; Key and Dunmore, 2015). Our results suggest that hammerstone use during
611 marrow acquisition and flake production would likely have resulted in the strongest
612 selective pressures on the evolution of our hands (among the tool behaviors tested).
613 The profound benefits early humans could have derived from their abilities to make and
614 use sharp-edged stone tools have long been established, including increases in brain
615 and body mass, territorial expansion, and advances in protective and predatory

616 behaviors (e.g., Washburn, 1960; Aiello and Wheeler, 1995; Domínguez-Rodrigo et al.,
617 2005; Shea, 2007; Ambrose, 2010; Shea and Sisk, 2010; Navarrete et al., 2011). It is
618 thus fitting that the production of flakes is among the two behaviors that impose the
619 greatest loads on the digits, making it even more likely to have elicited an adaptive
620 response.

621 In comparison to stone tool making, marrow acquisition has received
622 considerably less consideration in regard to the role it may have played in the evolution
623 of the human digits and hand. However, our results demonstrate that pressures
624 resulting from marrow acquisition can be as high as or even higher than those imposed
625 by the production of stone flakes. The caloric benefits of marrow in the hominin diet are
626 well established (Bunn, 1986; Bunn and Kroll, 1986; Blumenschine and Madrigal, 1993;
627 Aiello and Wheeler, 1995; Milton, 2003). Furthermore, archaeological evidence
628 demonstrates that hominins were potentially using hammerstones to access long bone
629 marrow cavities as early as 3.39 Ma at Dikika, Ethiopia (McPherron et al., 2010; but see
630 Domínguez-Rodrigo et al., 2011), contemporaneous with or even prior to the earliest
631 evidence of stone tool production at 3.3 Ma (Harmand et al., 2015). Although there is
632 currently no evidence that chimpanzees use hammerstones to access marrow cavities,
633 rendering it premature to propose that the last common ancestor (LCA) of *Pan* and
634 humans engaged in similar behaviors, chimpanzees are well known to use
635 hammerstones to crack open nuts (Whiten et al., 2001; Carvalho et al., 2008) and those
636 living in the Taï National Park in Côte d'Ivoire have been observed using sticks to pick
637 marrow out of colobus monkey long bones (Boesch and Boesch-Acherman, 2000).

638 Bringing together our manual pressure results with archaeological evidence, we
639 support Marzke et al.'s (1998) hypothesis that the biomechanical loads resulting from
640 marrow acquisition with a hammerstone may have also been a primary cause of
641 selection for greater stability and enhanced gripping abilities (e.g., a longer thumb
642 relative to finger length; Alba et al., 2003; but see Rolian and Gordon, 2013, 2014) in
643 early hominins' hands. Given the antiquity of the potentially percussed and cut-marked
644 bones from Dikika, Ethiopia (McPherron et al., 2010; but see Domínguez-Rodrigo et al.
645 2011) and percussive and marrow acquisition behaviors in extant chimpanzees (Boesch
646 and Boesch-Acherman, 2000; Carvalho et al., 2008), stone tool mediated marrow
647 acquisition may have exerted selective pressures on hominin digital and hand anatomy
648 just as early, if not even earlier, than those pressures related to flake production.

649 Our results also highlight that not all percussive behaviors may have been
650 equally likely to generate a selective pressure on the digits. In contrast to flake
651 production and marrow acquisition, the consistently low pressure experienced by the
652 digits as a group during nut-cracking suggests that this behavior may not have
653 generated strong selective pressures on digital morphology during human evolution.
654 Chimpanzees do not show significant anatomical adaptations for manual manipulation
655 or to withstand forces oriented in the same directions experienced by humans during
656 percussive behaviors (Tocheri et al., 2005; Marzke et al., 2010; Rolian et al., 2011), so
657 such adaptations would not be expected for purely nut-cracking hominins either. Recent
658 analyses of Early Pleistocene anvils from Olduvai Gorge have demonstrated
659 widespread percussive food processing activities by Lower Palaeolithic hominins,
660 including potential evidence of nut-cracking (Sánchez Yustos et al., 2015; Arroyo and

661 de la Torre, 2016; Arroyo et al., 2016). Assemblages of pitted hammerstones, anvils,
662 and nut debris from the Early-Middle Pleistocene Acheulean site of Gesher Benot
663 Ya'aqov (Israel) also provide early evidence of hominin nut-cracking behaviors (Goren-
664 Inbar et al., 2002). Furthermore, a 4,300 year old chimpanzee nut-cracking site in Tai
665 National Park (Mercader et al., 2007) and abundant documentation of chimpanzees in
666 central and western Africa using hammerstones to crack open a variety of nut types
667 (Whitesides, 1985; Whiten et al., 1999; Boesch and Boesch-Acherman, 2000; Carvalho
668 et al., 2008) suggest that the *Pan-Homo* LCA may have also used hammerstones to
669 crack open nut shells and access the internal nut meat (Haslam et al., 2009). Yet
670 derived morphological features of the hand thought to be related to increased dexterity
671 and/or manual loading are not known until *Australopithecus* (Tocheri et al., 2008),
672 several million years after a potential nut-cracking LCA.

673 The estimated caloric benefits of nut-cracking are enormous: Tai chimpanzees
674 obtain more than 3,000 calories per day by consuming the nuts they crack (Boesch and
675 Boesch Acherman, 2000) and maintain a 1:9 energy expenditure to calorie intake ratio
676 (Günther and Boesch, 1993). This ratio is impressive given the toughness values of the
677 nuts they consume. Boesch and Boesch-Acherman (2000) reported that cracking open
678 a panda nut (*Panda oleosa*) necessitated the equivalent of dropping a 10 kg stone from
679 a height of 120 cm. That this behavior has not led to the development of a digit and
680 hand anatomy more similar to our own—marked by large joint surface areas (Rolian et
681 al., 2011) and features contributing to robusticity and palmar stability (Marzke and
682 Marzke, 1987; Susman, 1994; Marzke et al., 1998; Ward et al., 2014)—suggests that
683 the loads and biomechanics associated with nut-cracking may be insufficient to induce

684 an adaptive anatomical response, or that they may already be accommodated by
685 chimpanzee digit and hand morphology.

686 It is important to consider the limitations present in the current study when
687 applying these results to interpretations of the hominin fossil record. The pressure
688 sensors quantify normal (i.e., vertical) force only, and thus forces acting in other planes
689 that may vary depending on the tool and grip used, are not included in this analysis.
690 Furthermore, pressure data were recorded from the palmar surfaces of the digits of the
691 dominant hand and therefore these data do not account for loads acting on the medial
692 and lateral sides of the digits or on the palm. Additionally, none of the participants in this
693 study had any prior experience making or using Plio-Pleistocene tools. The selection of
694 a novice population was deliberate to reduce the confounding effects of interparticipant
695 variation in experience across all of the behaviors and inter-behavior variation in
696 experience in a single participant. However, it is likely that the biomechanics presented
697 here would change over time with practice (Bril et al., 2012; Rein et al. 2014). Thus, the
698 data and the associated biomechanics and joint strains may represent a temporary
699 phase in skill acquisition rather than a constant. On the other hand, it is a phase that all
700 tool makers and users pass through and we cannot say whether digit selection was
701 responding to a particular stage in development or the cumulative effects, and if so
702 which stage that may be. Finally, we intentionally constrained the parameters of each
703 behavior in an effort to standardize data collection and ensure comparable experiences
704 across participants were being compared. Thus, we recognize that performing such
705 behaviors in a natural context would likely invoke a greater range of variation in grip
706 strategies, tool use/production techniques and manual pressures that are not captured

707 in this study. However, as the first comprehensive study of manual pressures during a
708 large variety of Plio-Pleistocene stone tool behaviors, these data provide the much
709 needed comparative data to develop more informed hypotheses about the manipulative
710 selective pressures that influence the evolution of human digit morphology.

711

712 **Conclusions**

713 Stone tool behaviors are not characterized by a single manual pressure
714 distribution pattern: behavior has a strong effect on relative and absolute load
715 distributions. Thus, in evaluations of behaviors likely to have exerted a selective
716 response across the digits, it is insufficient to consider load distribution in the absence
717 of load magnitude between behaviors (e.g., Williams et al., 2012; Key and Dunmore,
718 2015). When magnitude is taken into account, analyses of the digits as a group, of
719 individual digits and of phalanges point to hammerstone use during marrow acquisition
720 and flake production as the best candidates among the tested stone tool behaviors that
721 may have exerted primary selective pressures on the evolution of the human digits.

722

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731

732 **References**

733

734 Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the
735 digestive system in human and primate evolution. *Current Anthropology* 36, 199–
736 221.

737 Alba, D.M., Moyà-Solà, S., Köhler, M., 2003. Morphological affinities of the
738 *Australopithecus afarensis* hand on the basis of manual proportions and relative
739 thumb length. *Journal of Human Evolution* 44, 225–254.

740 Almécija, S., Alba, D.M., 2014. On manual proportions and pad-to-pad precision
741 grasping in *Australopithecus afarensis*. *Journal of Human Evolution* 73, 88–92.

742 Ambrose, S.H., 2010. Coevolution of composite-tool technology, constructive memory
743 and language: Implications for the evolution of modern human behavior. *Current*
744 *Anthropology* 51, S135–S137.

745 Arroyo, A., De La Torre, I., 2016. Assessing the function of pounding tools in the Early
746 Stone Age: a microscopic approach to the analysis of percussive artefacts from
747 Beds I and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science* 74,
748 23–34.

749 Arroyo, A., Hirata, S., Matsuzawa, T., De La Torre, I., 2016. Nut cracking tools used by
750 captive chimpanzees (*Pan troglodytes*) and their comparison with Early Stone Age
751 percussive artefacts from Olduvai Gorge, *PLoS One* 11, e0166788.

752 Bello, S.M., Parfitt, S.A., Stringer, S., 2009. Quantitative micromorphological analyses of
753 cut marks produced by ancient and modern handaxes. *Journal of Archaeological*
754 *Science* 36, 1869–1880.

755 Bertram, J.E.A., Swartz, S.M., 1991. The ‘law of bone transformation’: a case of crying
756 Wolff? *Biological Reviews* 66, 245–273.

757 Biewener, A.A., 1993. Safety factors in bone strength. *Calcified Tissue International* 53,
758 S68–S74.

759 Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental
760 determinations of the timing of hominid and carnivore access to long bones at FLK
761 *Zinjanthropus*, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29, 21–51.

762 Blumenschine, R.J., Madrigal, C., 1993. Variability in long bone marrow yields of East
763 African ungulates and its zooarchaeological implications. *Journal of Archaeological*
764 *Science* 20, 555–587.

765 Blumenschine, R.J., Pobiner, B.L., 2007. Zooarchaeology and the ecology of Oldowan
766 hominin carnivory. In: Ungar, P. (Ed.), *Evolution of the Human Diet: The Known,*
767 *the Unknown and the Unknowable*. Oxford University Press, Oxford, pp. 167–190.

768 Blumenschine, R.J., Whiten, A., Hawkes, K., 1991. Hominid carnivory and foraging
769 strategies, and the socio-economic function of early archaeological sites [and
770 discussion]. *Philosophical Transactions of the Royal Society London B* 334, 211–
771 221.

772 Boesch, C., Boesch-Acherman, H., 2000. *The Chimpanzees of the Tai Forest:*
773 *Behavioural Ecology and Evolution*. Oxford University Press, Oxford.

774 Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave
775 Taphonomy. University of Chicago Press, Chicago.

776 Braun, D.R., Harris, J.W.K., Levin, N.E., McCoy, J.T., Herries, A.I.R., Bamford, M.K.,
777 Bishop, L.C., Richmond, B.G., Kibunjia, M., 2010. Early hominin diet included
778 diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya.
779 Proceedings of the National Academy of Sciences 107, 10002–10007.

780 Braun, D.R., Plummer, T., Ferraro, J.V., Ditchfield, P., Bishop, L.C., 2009. Raw material
781 quality and Oldowan hominin toolstone preferences: evidence from Kanjera South,
782 Kenya. Journal of Archaeological Science 36, 1605–1614.

783 Bril, B., Rein, R., Nonaka, T., 2010. The role of expertise in tool use: skill differences in
784 functional action adaptations to task constraints. Journal of Experimental
785 Psychology 36, 825–839.

786 Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata,
787 S., Roux, V., 2012. Functional mastery of percussive technology in nut-cracking
788 and stone-flaking actions: experimental comparison and implications for the
789 evolution of the human brain. Philosophical Transactions of the Royal Society
790 London B 367, 59–74.

791 Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene
792 hominids from Koobi Fora and Olduvai Gorge. Nature 291, 574–577.

793 Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities
794 at Olduvai Gorge, Tanzania and Koobi Fora, Kenya. Journal of Human Evolution
795 15, 673–690.

796 Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/Pleistocene hominids at
797 Olduvai Gorge, Tanzania. *Current Anthropology* 27, 431–452.

798 Burr, D.B., 1985. Bone remodelling in response to in vivo fatigue microdamage. *Journal*
799 *of Biomechanics* 18, 189–200.

800 Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., 2008. Chaînes opératoires and
801 resource-exploitation strategies in chimpanzee *Pan troglodytes* nut cracking.
802 *Journal of Human Evolution* 55, 148–163.

803 Chai, H., Lawn, B.R., 2007a. A Universal relation for edge chipping from sharp contacts
804 in brittle materials: a simple means of toughness evaluation. *Acta Materialia* 55,
805 2555–2561.

806 Chai, H., Lawn, B.R., 2007b. Edge chipping of brittle materials: effect of side-wall
807 inclination and loading angle. *International Journal of Fracture* 145, 159–165.

808 Chao, E., An, K.-N., Cooney, W. III, Linscheid, P., 1989. *Biomechanics of the Hand*.
809 World Scientific, Singapore.

810 Clark, J.L., Plug, I., 2008. Animal exploitation strategies during the South African Middle
811 Stone Age: Howiesons Poort and post-Howiesons Poort fauna from Sibudu Cave.
812 *Journal of Human Evolution* 54, 886–898.

813 Cooney, W. III, Chao, E., 1977. Biomechanical analysis of static forces in the thumb
814 during hand function. *Journal of Bone and Joint Surgery* 59, 27–36.

815 Darwin, C., 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray,
816 London.

817 de Heinzelin, J., Desmond Clark, J., White, T., Hart, W., Renne, P.R., WoldeGabriel, G.,
818 Bevene, Y., Vrba, E.S., 1999. Environment and behavior of 2.5-million-year-old
819 Bouri hominids. *Science* 283, 625–629.

820 Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22
821 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using
822 cut-mark data. *Journal of Human Evolution* 33, 669–690.

823 Domínguez-Rodrigo, M., Pickering, T.R., Bunn, H.T., 2011. Reply to McPherron et al.:
824 Doubting Dikika is about data, not paradigms. *Proceedings of the National*
825 *Academy of Sciences* 108, E117.

826 Domínguez-Rodrigo, M., Pickering, T.R., Semaw, S., Rogers, J.J. 2005. Cutmarked
827 bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: implications for
828 the function of the world's oldest stone tools. *Journal of Human Evolution* 48, 109–
829 121.

830 Domínguez-Rodrigo, M., Serrallonga, J., Juan-Tresserras, J., Alcalá, L., Luque, L.,
831 2001. Woodworking activities by early humans: a plant residue analysis on
832 Acheulian stone tools from Peninj (Tanzania). *Journal of Human Evolution* 40,
833 289–299.

834 Frost, H.M., 1987. Bone “mass” and the “mechanostat”: A proposal. *Anatomical Record*
835 219, 1–9.

836 Goren-Inbar, N., Sharon, G., Melamed, Y., Kislev, M., 2002. Nuts, nut cracking, and
837 pitted stones at Gesher Benot Ya’aqov, Israel. *Proceedings of the National*
838 *Academy of Sciences* 99, 2455–2460.

839 Green, D.J., Gordon, A.D., 2008. Metacarpal proportions in *Australopithecus africanus*.
840 Journal of Human Evolution 54, 705–719.

841 Günther, M.M., Boesch, C., 1993. Energetics of nut-cracking behaviour in wild
842 chimpanzees. In: Preuschoft, H., Chivers, D.J. (Eds.), Hands of Primates.
843 Springer, Vienna, pp. 109–129.

844 Hamrick, M., Churchill, S., Schmitt, D., Hylander, W., 1998. EMG of the human flexor
845 pollicis longus muscle: implications for the evolution of hominid tool use. Journal of
846 Human Evolution 34, 123–136.

847 Harmand, S., Lewis, J.E., Feibel, C.S., Lepre, C.J., Prat, S., Lenoble, A., Boes, X.,
848 Quinn, R.L., Brenet, M., Arroyo, A., Taylor, N., Clement, S., Daver, G., Brugal, J.-
849 P., Leakey, L., Mortlock, R.A., Wright, J.D., Lokorodi, S., Kirwa, C., Kent, D.V.,
850 Roche, H., 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana,
851 Kenya. Nature 521, 310–315.

852 Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano,
853 A., Du, A., Hardy, B., Harris, J., Marchant, L., 2009. Primate archaeology. Nature
854 460, 339–344.

855 Hohmann, G., Fruth, B., 2003. Culture in bonobos? Between-species and within species
856 variation in behavior. Current Anthropology 44, 563–571.

857 Jennings, J.S., MacMillan, N.H., 1986. A tough nut to crack. Journal of Materials
858 Science, 21, 1517-1524.

859 Key, A.J., 2016. Manual loading distribution during carrying behaviors: implications for
860 the evolution of the hominin hand. PLoS One 11, e0163801.

861 Key, A.J., Dunmore, C.J., 2015. The evolution of the hominin thumb and the influence
862 exerted by the non-dominant hand during stone tool production. *Journal of Human*
863 *Evolution* 78, 60–69.

864 Key, A.J., Dunmore, C.J., Hatala, K.G., Williams-Hatala, E.M., 2017. Flake morphology
865 as a record of manual pressure during stone tool production. *Journal of*
866 *Archaeological Science: Reports* 12, 43–53.

867 Key, A.J., Lycett, S.J., 2017. Investigating interrelationships between Lower Palaeolithic
868 stone tool effectiveness and tool user biometric variation: implications for
869 technological and evolutionary changes. *Archaeological and Anthropological*
870 *Sciences* DOI: 10.1007/s12520-016-0433-x

871 Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z.,
872 Marean, C.W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., 1996. Late Pliocene
873 *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member),
874 Ethiopia. *Journal of Human Evolution* 31, 549–561.

875 Kivell, T.L., 2015. Evidence in hand: recent discoveries and the early evolution of
876 human manual manipulation. *Philosophical Transactions of the Royal Society*
877 *London B* 370, 201501505.

878 Kivell, T.L., 2016. A review of trabecular bone functional adaptation: what have we
879 learned from trabecular analyses in extant hominoids and what can we apply to
880 fossils? *Journal of Anatomy* 228, 569–594.

881 Kivell, T.L., Kibii, J.M., Churchill, S.E., Schmid, P., Berger, L.R., 2011. *Australopithecus*
882 *sediba* hand demonstrates mosaic evolution of locomotor and manipulative
883 abilities. *Science* 333, 1411–1417.

884 Klein, R.G., 1976. The mammalian fauna of the Klasies River Mouth Sites, Southern
885 Cape Province, South Africa. *South African Archaeological Bulletin* 31, 75–98.

886 Kopperdahl, D.L., Keaveny, T.M., 1998. Yield strain behavior of trabecular bone.
887 *Journal of Biomechanics* 31, 601–608.

888 Leakey, L.S., Tobias, P.V., Napier, J.R., 1964. A new species of the genus *Homo* from
889 Olduvai Gorge. *Nature* 202, 7–9.

890 Lorenzo, C., Arsuaga, J.L., Carretero, J.M., 1999. Hand and foot remains from the Gran
891 Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *Journal of Human*
892 *Evolution* 37, 501–522.

893 Lovejoy, C.O., Simpson, S.W., White, T.D., Asfaw, B., Suwa, G., 2009. Careful climbing
894 in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive.
895 *Science* 326, 70e1–70e8.

896 Lucas, P.W. 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge
897 University Press, Cambridge.

898 Lucas, P.W., Gaskins, J.T., Lowrey, T.K., Harrison, M.E., Morrogh-Bernard, H.C.,
899 Cheyne, S.M., Begley, M.R., 2011. Evolutionary optimization of material properties
900 of a tropical seed. *Journal of the Royal Society Interface*, rsif20110188.

901 Lycett, S.J., von Cramon-Taubadel, N., 2008. Acheulean variability and hominin
902 dispersals: a model-bound approach. *Journal of Archaeological Science* 35, 553–
903 562.

904 Marzke, M.W., 1997. Precision grips, hand morphology, and tools. *American Journal of*
905 *Physical Anthropology* 102, 91–110.

906 Marzke, M.W., Marzke, R.F., 1987. The third metacarpal styloid process in humans:
907 origin and functions. *American Journal of Physical Anthropology* 73, 415–431.

908 Marzke, M.W., Shackley, M.S., 1986. Hominid hand use in the Pliocene and
909 Peistocene: evidence from experimental archaeology and comparative
910 morphology. *Journal of Human Evolution* 16, 439–460.

911 Marzke, M.W., Tocheri, M.W., Steinberg, B., Femiani, J.D., Reece, S.P., Linscheid,
912 R.L., Orr, C.M., Marzke, R.F. 2010. Comparative 3D quantitative analyses of
913 trapeziometacarpal joint surface curvatures among living catarrhines and fossil
914 hominins. *American Journal of Physical Anthropology* 141, 38–51.

915 Marzke, M.W., Toth, N., Schick, K., Reece, S., Steinberg, B., Hunt, K., Linscheid, R.,
916 An, K., 1998. EMG study of hand muscle recruitment during hard hammer
917 percussion manufacture of Oldowan tools. *American Journal of Physical*
918 *Anthropology* 105, 315–332.

919 McPherron, S.P., Alemseged, Z., Marean, C.W., Wynn, J.G., Reed, D., Geraads, D.,
920 Bobe, R., Béarat, H.A., 2010. Evidence for stone-tool-assisted consumption of
921 animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466, 857–
922 860.

923 McPoil, T.G., Cornwall, M.W., Yamada, W., 1995. A comparison of two in-shoe plantar
924 pressure measurement systems. *The Lower Extremity* 2, 95–103.

925 Mercader, J., Barton, H., Gillespie, J., Harris, J.M., Kuhn, S.L., Tyler, R., Boesch, C.,
926 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone
927 technology. *Proceedings of the National Academy of Sciences* 104, 3043–3048.

928 Milton, K., 2003. The critical role played by animal source foods in human (*Homo*)
929 evolution. *The Journal of Nutrition* 133, 3886S–3892S.

930 Napier, J., 1956. The prehensile movements of the human hand. *The Journal of Bone*
931 *and Joint Surgery* 38, 902–913.

932 Napier, J., 1962. Fossil hand bones from Olduvai Gorge. *Nature* 196, 409–411.

933 Navarrete, A., van Schaik, C.P., Isler, K., 2011. Energetics and the evolution of human
934 brain size. *Nature* 480, 91–93.

935 Neufuss, J., Humle, T., Cremaschi, A., Kivell, T.L., 2017. Nut-cracking behaviour in wild-
936 born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-
937 preference, hand grips and efficiency. *American Journal of Primatology* 79, 1–16.

938 Niewoehner, W.A., 2001. Behavioral inferences from the Skhul/Qafzeh early modern
939 human hand remains. *Proceedings of the National Academy of Sciences* 98,
940 2979–2984.

941 Price, C., Parker, D., Nester, C., 2016. Validity and repeatability of three in-shoe
942 pressure measurement systems. *Gait & Posture* 46, 69–74.

943 Putti, A.B., Arnold, G.P., Cochrane, L., Abboud, R.J., 2007. The Pedar[®] in-shoe system:
944 repeatability and normal pressure values. *Gait & Posture* 25, 403–405.

945 R Core Team, 2017. R: A language and environment for statistical computing. R
946 Foundation for Statistical Computing, Vienna.

947 Rein, R., Nonaka, T., Bril, B., 2014. Movement pattern variability in stone knapping:
948 implications for the development of percussive technologies. *PLoS One* 9,
949 e113567.

950 Rhodes, J.A., Churchill, S.E., 2009. Throwing in the Middle and Upper Paleolithic:
951 inferences from an analysis of humeral retroversion. *Journal of Human Evolution*
952 56, 1–10.

953 Roach, N.T., Richmond, B.G., 2015. Clavicle length, throwing performance and the
954 reconstruction of the *Homo erectus* shoulder. *Journal of Human Evolution* 80,
955 107–113.

956 Roche, H., Delagnes, A., Brugal, J.-B., Fiebel, C.S., Kibunjia, M., Mourrell, V., Texier,
957 P.-J., 1999. Early hominid stone tool production and technical skill 2.34 Myr ago in
958 West Turkana, Kenya. *Nature* 399, 57–60.

959 Roffman, I., Savage-Rumbaugh, S., Rubert-Pugh, E., Ronen, A., Nevo, E., 2006. Stone
960 tool production and utilization by bonobo-chimpanzees (*Pan paniscus*). *Proceedings*
961 *of the National Academy of Sciences* 109, 14500–14503.

962 Rolian, C., Gordon, A.D., 2013. Reassessing manual proportions in *Australopithecus*
963 *afarensis*. *American Journal of Physical Anthropology* 152, 393–406.

964 Rolian, C., Gordon, A.D., 2014. Response to Almécija and Alba (2014) – On manual
965 proportions in *Australopithecus afarensis*. *Journal of Human Evolution* 73, 93–97.

966 Rolian, C., Lieberman, D.E., Hallgrímsson, B., 2010. The coevolution of human hands
967 and feet. *Evolution* 64, 1558–1568.

968 Rolian, C., Lieberman, D.E., Zermeno, J.P., 2011. Hand biomechanics during simulated
969 stone tool use. *Journal of Human Evolution* 61, 26–41.

970 Rubin, C.T., Lanyon, L.E., 1985. Regulation of bone mass by mechanical strain
971 magnitude. *Calcified Tissue International* 37, 411–417.

972 Sánchez Yustos, P., Diez-Martín, F., Díaz, I.M., Duque, J., Fraile, D., Domínguez, M.,
973 2015. Production and use of percussive stone tools in the Early Stone Age:
974 Experimental approach to the lithic record of Olduvai Gorge, Tanzania. *Journal of*
975 *Archaeological Science: Reports* 2, 367–383.

976 Semaw, S., 2000. The world's oldest stone artefacts from Gona, Ethiopia: their
977 implications for understanding stone technology and patterns of human evolution
978 between 2.6–1.5 million years ago. *Journal of Archaeological Science* 27, 1197–
979 1213.

980 Sharon, G., 2008. Large flake Acheulian. *Quaternary International* 223–224, 226–233.

981 Shea, J.J., 2007. Lithic technology, or, what stone tools can (and can't) tell us about
982 early hominin diets. In: Ungar, P.S. (Ed.), *Evolution of the Human Diet: The*
983 *Known, the Unknown, and the Unknowable*. Oxford University Press, Oxford, pp.
984 212–229.

985 Shea, J.J., Sisk, M.L., 2010. Complex projectile technology and *Homo sapiens* dispersal
986 into Western Eurasia. *PaleoAnthropology* 2010, 100–122.

987 Skinner, M.M., Stephens, N.B., Tsegai, Z.J., Foote, A.C., Nguyen, N.H., Gross, T.,
988 Pahr, D.H., Hublin, J.J., Kivell, T.L., 2015. Human-like hand use in
989 *Australopithecus africanus*. *Science* 347, 395–399.

990 Stout, D., Semaw, S., Rogers, M.J., Cauche, D., 2010. Technological variation in the
991 earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution* 58, 474–
992 491.

993 Stout, D., Toth, N., Schick, K., Chaminade, T., 2008. Neural correlates of Early Stone
994 Age toolmaking: technology, language and cognition in human evolution.
995 Proceedings of the National Academy of Sciences 363, 1939–1949.

996 Susman, R.L., 1988. Hand of *Paranthropus robustus* from Member 1, Swartkrans: fossil
997 evidence for tool behavior. Science 240, 781–784.

998 Susman, R.L., 1994. Fossil evidence for early hominid tool use. Science 265, 1570–
999 1573.

1000 Susman, R.L., 1998. Hand function and tool behavior in early hominids. Journal of
1001 Human Evolution 35, 23–46.

1002 Tocheri, M.W., Orr, C.M., Jacofsky, M.C., Marzke, M.W., 2008. The evolutionary history
1003 of the hominin hand since the last common ancestor of *Pan* and *Homo*. Journal of
1004 Anatomy 212, 544–562.

1005 Tocheri, M.W., Razdan, A., Williams, R.C., Marzke, M.W. 2005. A 3D quantitative
1006 comparison of trapezium and trapezoid relative articular and nonarticular surface
1007 areas in modern humans and great apes. Journal of Human Evolution 49, 570–
1008 586.

1009 Toth, N., 1985. The Oldowan reassessed: A close look at early stone artifacts. Journal
1010 of Archaeological Science 12, 101–120.

1011 Toth, N., Schick, K.D., Savage-Rumbaugh, E.S., Sevcik, R.A., Rumbaugh, D.M., 1993.
1012 *Pan* the tool-maker: investigations into the stone tool-making and tool-using
1013 capabilities of a bonobo (*Pan paniscus*). Journal of Archaeological Science 20,
1014 81–91.

1015 Unger, P., Grine, F.E., Teaford, M.F., 2006. Diet in early *Homo*: A review of the
1016 evidence and a new model of adaptive versatility. *Annual Review of Anthropology*
1017 35, 209–228.

1018 Ward, C.V., Tocheri, M.W., Plavcan, J.M., Brown, F.H., Manthi, F.K., 2014. Early
1019 Pleistocene third metacarpal from Kenya and the evolution of modern human-like
1020 hand morphology. *Proceedings of the National Academy of Sciences* 111, 121–
1021 124.

1022 Washburn, S.L., 1960. Tools and human evolution. *Scientific American* 203, 62–75.

1023 Weiss, K.M., 2012. Agnotology. *Evolutionary Anthropology* 21, 96–100.

1024 Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin,
1025 C.E., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. *Nature* 399,
1026 682–685.

1027 Whitesides, G.H., 1985. Nut-cracking by wild chimpanzees in Sierra, Leone, West
1028 Africa. *Primates* 26, 91–94.

1029 Williams, E.M., Gordon, A.D., Richmond, B.G., 2012. Hand pressure distribution during
1030 Oldowan stone tool production. *Journal of Human Evolution* 62, 520–532.

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1032 **Figure captions**

1033 **Figure 1.** Dorsal (left) and palmar (right) views of the sensor and cable placement and
1034 the attachment apparatus.

1035 **Figure 2.** Heat map showing the distribution across the digits of normalized pressures.
1036 The lowest normalized pressures acting at each sensor are shown in blue, the highest
1037 normalized pressures acting at each sensor are shown in red (refer to the scale on the

1038 right). The highest normalized pressures tended to act on digit I and lowest normalized
1039 pressures tended to act on the digit V. Otherwise, there was considerable variation in
1040 the distribution. An a priori example of similarity is provided at the left. Abbreviations:
1041 HA = handaxe; see Table 1 for sensor abbreviations.

1042 **Figure 3.** Boxplots displaying the raw cumulative pressures acting on the hand during
1043 the tested behaviors. The center line represents the sample median. The box
1044 boundaries display the interquartile range (25–75%), and whiskers extend to the
1045 farthest data points that are within 1.5 times the interquartile range from either the lower
1046 or upper bound of the box. Dots represent extreme outliers, defined as points more than
1047 1.5 times the interquartile range from the central 50% of the data.

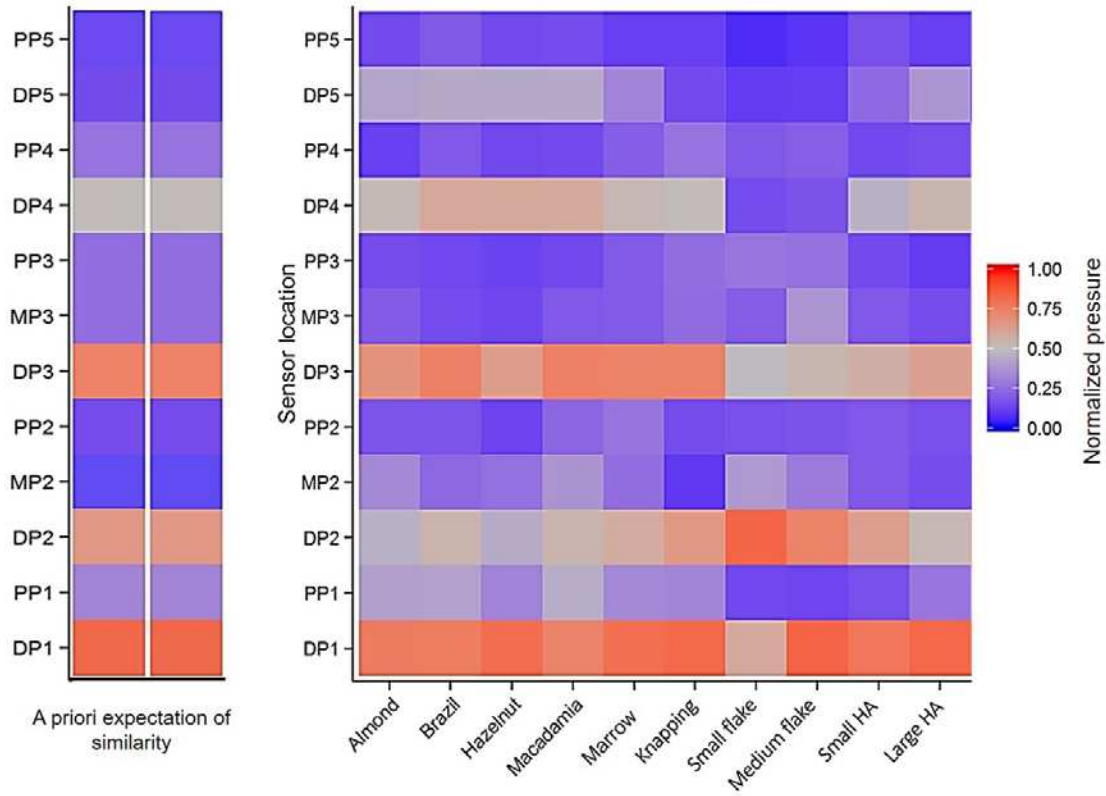
1048 **Figure 4.** Heat map showing the distribution of raw pressures among the digits. The
1049 lowest absolute pressures acting along each digit are shown in blue, the highest
1050 absolute pressures acting along each digit are shown in red (refer to the scale on the
1051 right). Across all behaviors, absolute pressures were highest on digit I and lowest on
1052 digit V. Marrow acquisition and flake production tended to impose significantly greater
1053 loads on the digits compared with other tested behaviors. Abbreviations: HA = handaxe.

1054 **Figure 5.** Heat map showing the distribution of raw pressures among the phalanges.
1055 The lowest absolute pressures acting along each sensor are shown in blue, the highest
1056 absolute pressures acting along each sensor are shown in red (refer to the scale on the
1057 right). Pressures tended to be highest on the distal phalanges and marrow acquisition
1058 and flake production tended to impose significantly greater loads on each phalangeal
1059 segment compared with other tested behaviors. Abbreviations: HA = handaxe; see
1060 Table 1 for sensor abbreviations.



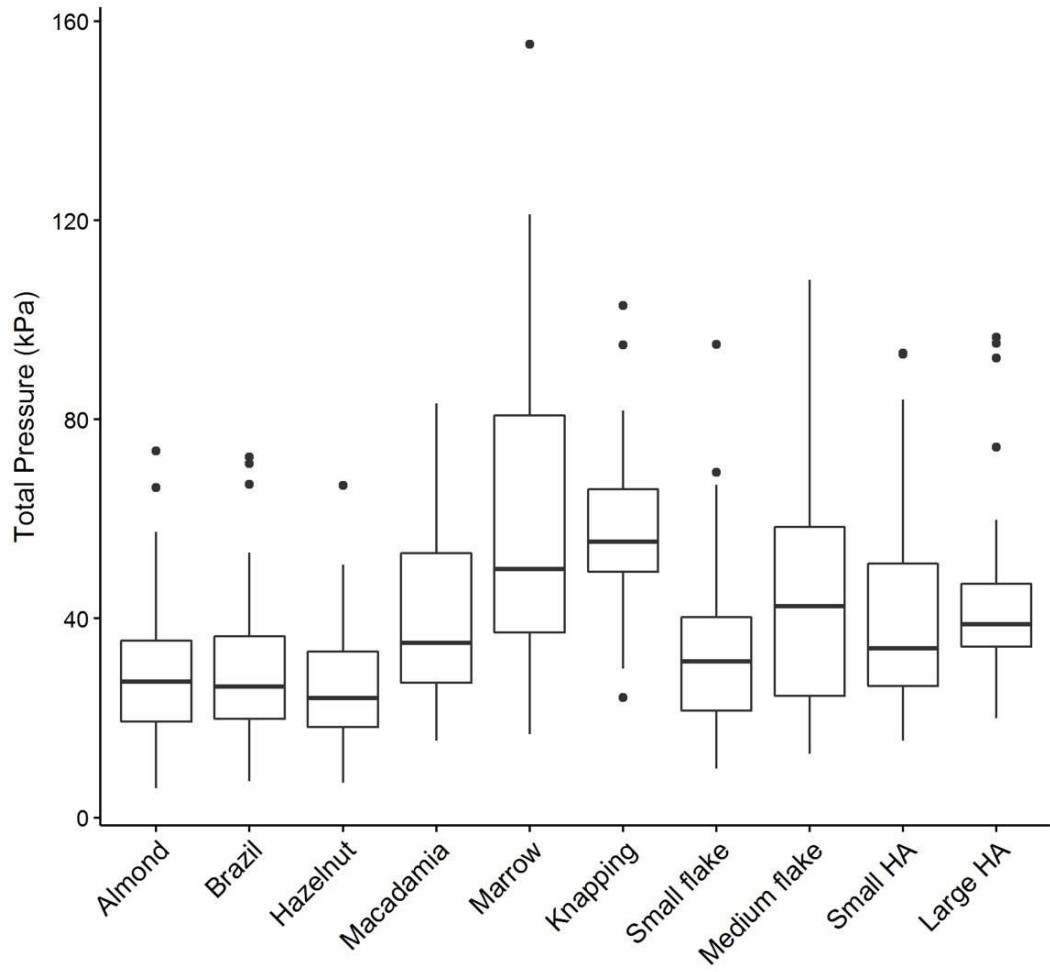
1061

1062 **Figure 1**



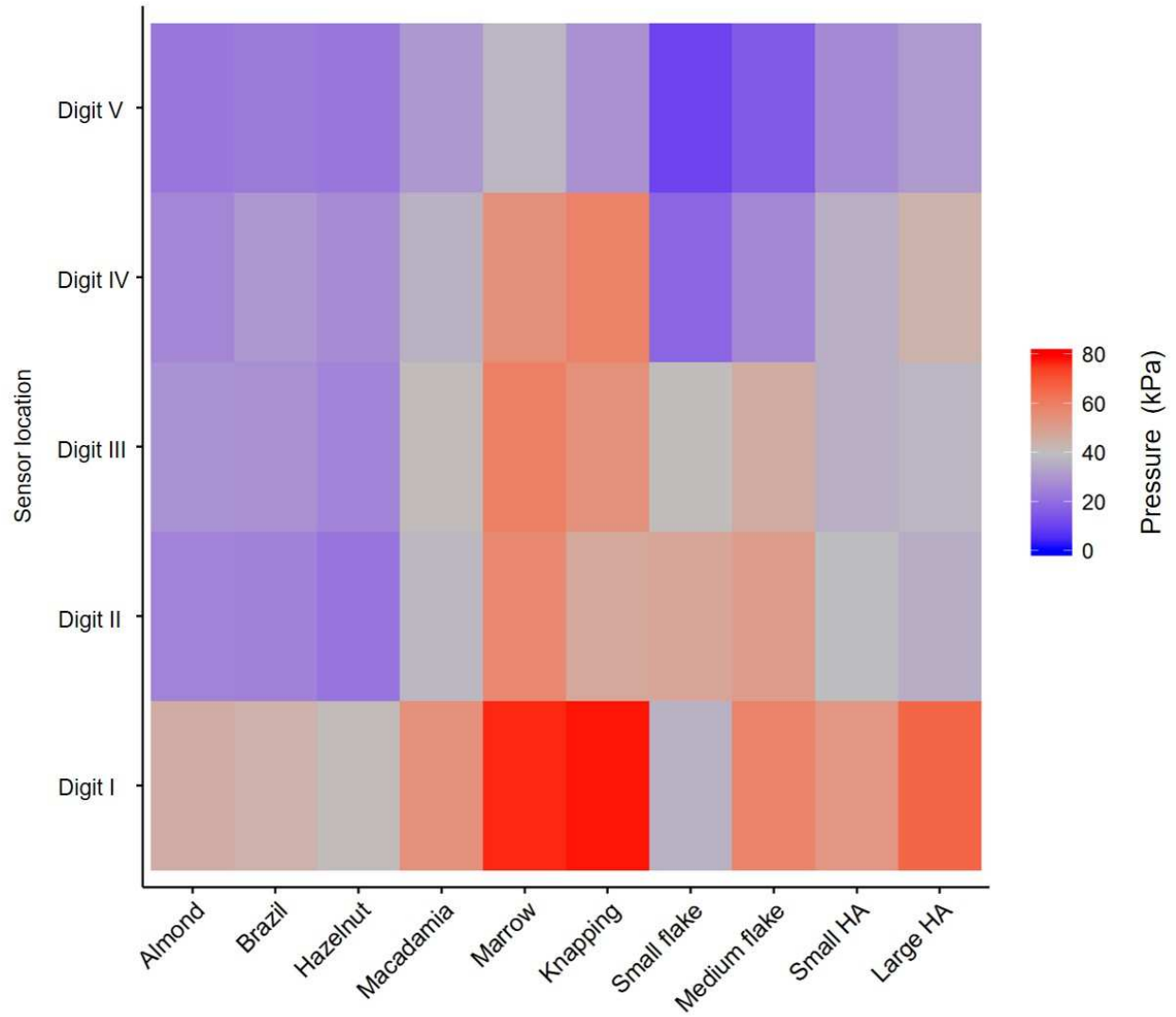
1063

1064 **Figure 2**



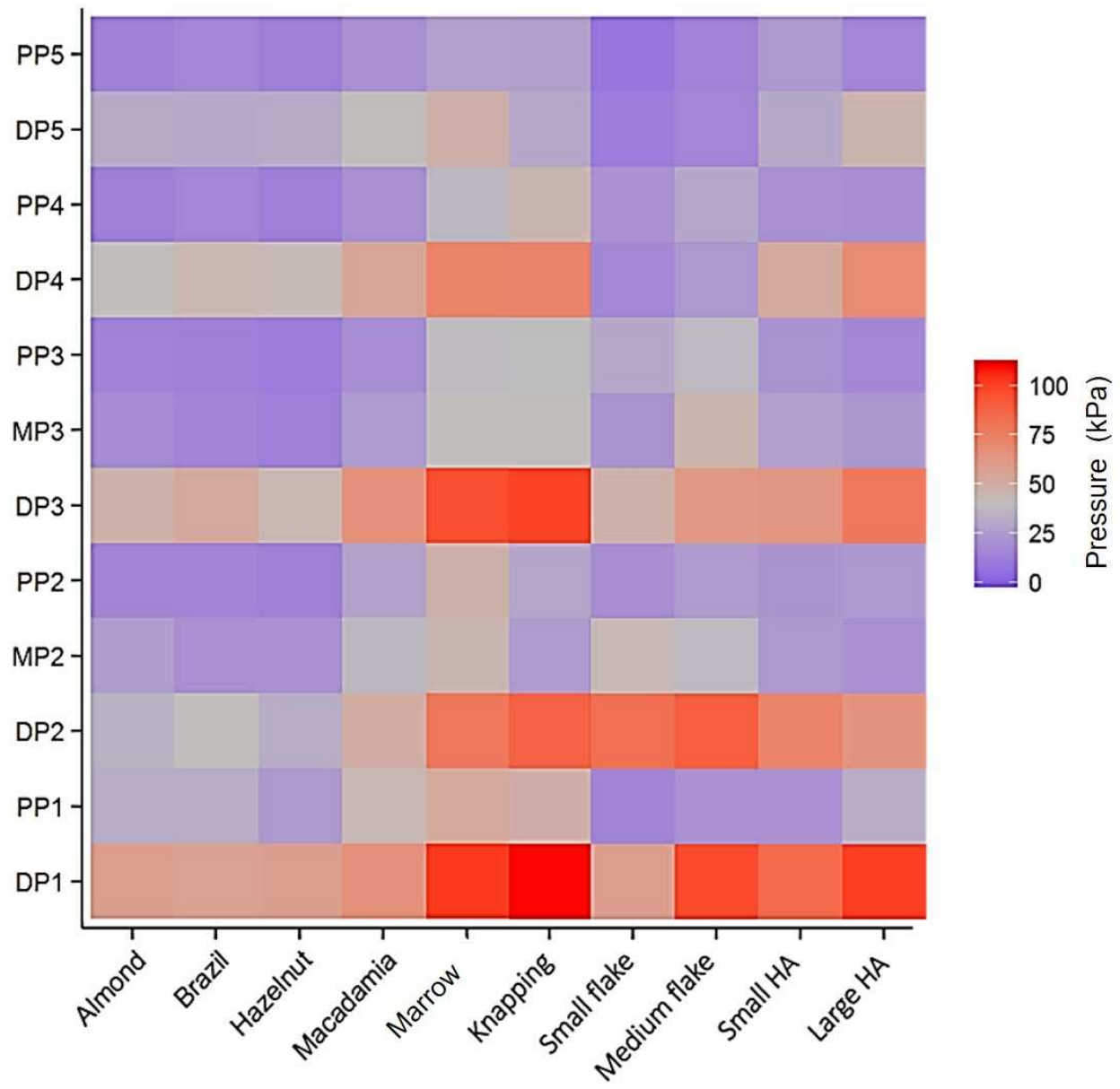
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1066 **Figure 3**



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1068 **Figure 4**



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1070 **Figure 5**

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1072 **Table 1** Sensor placement.

1073

Phalanx	Abbreviation ¹⁰⁷⁴
First distal phalanx	DP1 ¹⁰⁷⁵
First proximal phalanx	PP1 ¹⁰⁷⁶
Second distal phalanx	DP2 ¹⁰⁷⁷
Second middle phalanx	MP2 ¹⁰⁷⁸
Second proximal phalanx	PP2 ¹⁰⁷⁹
Third distal phalanx	DP3 ¹⁰⁸⁰
Third middle phalanx	MP3 ¹⁰⁸¹
Third proximal phalanx	PP3 ¹⁰⁸²
Fourth distal phalanx	DP4 ¹⁰⁸³
Fourth proximal phalanx	PP4 ¹⁰⁸⁴
Fifth distal phalanx	DP5 ¹⁰⁸⁵
Fifth proximal phalanx	PP5 ¹⁰⁸⁶

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1091 **Table 2** Descriptive stone tool metrics

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Tool		Mean	SD	CV 1093
Small	Mass (g)	5.6	1.5	26.7 1094
flake	Length (mm)	29.2	0.5	1.8 1095
Medium	Mass (g)	29.8	7.1	23.7 1096
flake	Length (mm)	58.3	1.4	2.4 1097
Small	Mass (g)	235.4	59.2	25.2 1098
handaxe	Length (mm)	119.7	8.5	7.1 1099
Large	Mass (g)	756.7	229.3	30.3 1100
handaxe	Length (mm)	168.4	18.9	11.2 1101

1102

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1104

1105 Abbreviations: CV = coefficient of variation (%); SD = standard deviation.

1106

1107

1108 **Table 3** Relationships between activity and normalized pressure distributions.

Sensor	F-value	$p (>F)$	1109
			1110
DP1	2.583	0.007	1111
PP1	7.749	< 0.001	1112
DP2	7.741	< 0.001	1113
MP2	4.883	< 0.001	1114
PP2	1.313	0.229	1115
DP3	4.291	< 0.001	1116
MP3	3.429	< 0.001	1117
PP3	4.137	< 0.001	1118
DP4	18.24	< 0.001	1119
PP4	1.993	0.039	1120
DP5	10.080	< 0.001	1121
PP5	1.890	0.052	1122
			1123

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1127 See Table 1 for sensor abbreviations.

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1136 **Table 4**1137 Linear mixed effects model fit to cumulative digital pressure.^a

	Value	SE	t-value	<i>p</i> -value
Intercept	29.621	2.888	10.257	0
Brazil	0.568	1.036	0.548	0.584
Hazelnuts	-2.664	1.035	-2.573	0.010
Macadamia	10.605	1.035	10.244	0
Marrow	29.641	0.903	32.843	0
Knapping	20.648	1.012	20.401	0
Small flake	5.157	1.045	4.933	0
Medium flake	16.153	1.045	15.452	0
Small handaxe	11.339	1.045	10.846	0
Large handaxe	15.084	1.045	14.428	0

1138 ^a Degrees of freedom = 4146.

1139

1140 **Table 5**

1141 Relationships between behavior and absolute inter-digital pressure distributions.

Sensor	F-value	$p (>F)$
Digit 1	11.405	< 0.001
Digit 2	9.152	< 0.001
Digit 3	7.614	< 0.001
Digit 4	11.895	< 0.001
Digit 5	6.901	< 0.001

1142

1143

1144 **Table 6**

1145 Relationships between behavior and absolute inter-sensor pressure distributions.

Sensor	F value	$p (>F)$
DP1	9.671	< 0.001
PP1	8.610	< 0.001
DP2	10.87	< 0.001
MP2	4.599	< 0.001
PP2	5.641	< 0.001
DP3	9.838	< 0.001
MP3	5.966	< 0.001
PP3	7.179	< 0.001
DP4	13.661	< 0.001
PP4	8.460	< 0.001
DP5	6.134	< 0.001
PP5	5.003	< 0.001

1146 See Table 1 for sensor abbreviations.

1147

1148