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Investigating interrelationships between Lower Palaeolithic stone tool effectiveness and tool user biometric variation: implications for technological and evolutionary changes

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Abstract

Lower Palaeolithic hominins are thought to have been dependent upon stone tools during the acquisition and processing of food resources. Hence, it is hypothesized that the evolutionary advantages provided by efficient stone tool use may have selected for anatomical changes observed in the hand during this period. Similarly, hominin manipulative capabilities are suggested to have been of consequence to Lower Palaeolithic technological choices and tool-use capabilities. The extent and character of these relationships are not, however, fully understood and it is not known whether these hypothesized co-evolutionary and co-dependent relationships are consistent across varying technological and task-type conditions. Here, six key biometric parameters of the hand are investigated in terms of their statistical relationship with cutting efficiency using both flakes and handaxes over extended periods of use and in multiple types of cutting task. Results indicate that (1) both handaxe and flake cutting efficiency is significantly related with biometric variation of individual tool-users, (2) relationships between biometric parameters and efficiency are consistent across extended durations but vary dependent upon task-type conditions, (3) manipulative strength is the most significant biometric trait in terms of predicting flake efficiency, while (4) hand size is the strongest predictor of handaxe cutting efficiency. These results demonstrate the long-term impact that stone tool use likely had on the evolution of hominin biometric variation during the Lower Palaeolithic, while also highlighting the variable influence of different tool use contexts. Most notably, results indicate that the onset of the Acheulean may have been dependent, a priori, upon hand dimensions that are close to the modern human range, and that prior to the appearance of this anatomy, handaxe use would have been an impractical (i.e. inefficient) tool use behaviour compared to the use of flakes.

1. Introduction

No living nonhuman animal has ever been known to intentionally produce a stone cutting tool in the wild (Shumaker et al., 2011). Although some nonhuman primates (Pan troglodytes and Sapajus libidinosus) may on occasion break stones through percussive behaviours, they do not subsequently use them for cutting (Mercader et al., 2007; Proffitt et al., 2016). Hence, the appearance of stone cutting technology, as far as we know, seems to be a uniquely hominin invention that arose during the course of human evolution (Roux and Bril, 2005). With the inauguration of such technology, the door was opened to a more 'plastic' world in which food, tools and equipment would eventually be cut, carved and modified by hominin populations across the globe. Lithic technology is thus considered to play a substantial role in the evolutionary history of humans, no more so than in the evolution of modern human upper limb anatomy and manipulative capabilities (Tocheri et al., 2008; Marzke, 2013; Kivell, 2015). Indeed, from the onset of the Oldowan at least 2.6 Mya (Semaw, 2000; Semaw et al., 2003) it is thought to have played a vital role in selecting for key anatomical traits that facilitate the secure, forceful, and yet dexterous manipulation of stone tools, hammer stones and stone cores (Marzke, 1997; Hamrick et al., 1998; Marzke et al., 1998; Key and Lycett, 2011; Rolian et al., 2011; Williams et al., 2012, 2014; Key and Dunmore, 2015).

Parsimony and the comparative approach suggest that hominins were engaged in tool use behaviours prior to the appearance of the first stone tools, with this most likely being linked to the extraction and processing of food resources (Panger et al., 2002; Marchant and McGrew, 2005; Hernandez-Aguillar et al., 2007; Duda and Zrzavý, 2013). As such, the first stone tool use is also likely to have been during the acquisition and processing of food resources. Indeed, following the onset of the Oldowan, evidence to support this inference is found in the form of cut-marked bones from medium-to-large-sized animals and lithic microwear traces suggestive of butchery processes (Bunn, 1981; Keeley and Toth, 1981; de Heinzelin et al., 1999; Semaw et al., 2003; Domínguez-Rodrigo et al. 2005; Braun et al. 2010; Plummer and Bishop, 2016). It is therefore evident that by 2.6 Mya, hominins were not only capably producing and utilising flake tools, but that there was necessity to do so when removing flesh from animal carcasses. Contrastingly, although some chimpanzee (Pan troglodytes) populations are famed for their hunting capabilities and appetite for meat, they do not actively employ tools in the processing and removal of flesh from their prey (Boesch and Boesch, 1989, 1990; Wynn and McGrew, 1989; McGrew, 1992; Pruetz and Bertolani, 2007; Newton-Fisher, 2014). The same is true for bonobo chimpanzee (P. paniscus) populations that also consume meat (Hohmann and Fruth, 2008). This lack of tool-assisted butchery cannot easily be attributed to a physical inability to produce or utilise stone flakes suitable for cutting (Wynn and McGrew, 1989; Toth et al., 1993; Schick et al., 1999; Mercader et al., 2002; Toth and Schick, 2009), but rather, it seems that there is a lack of incentive for this behavioural repertoire to naturally occur. Indeed, chimpanzee meat eating is characterised by the consumption of small-bodied vertebrates that can readily be dismembered through the bare force of hands and teeth (Boesch, 1994; McGrew, 1992; Stanford, 1996; Newton-Fisher, 2014; Marzke et al., 2015).

The onset of the Oldowan is thus likely linked to a substantial change in hominin behaviour and dietary composition; specifically, a greater premium was placed on animal food resources that necessitated the employment of a sharp cutting edge (Shipman and Walker, 1989; Ambrose, 2001; Shea, 2007). Moreover, cut-marked faunal remains not only suggest that Oldowan hominins were butchering large mammals, but that they were at times gaining early access to these resources (Domínguez-Rodrigo, 1997; Domínguez-Rodrigo et al., 2005; Ferraro et al., 2013). Hence, Oldowan hominins were, on occasion, required to cut through tough hide, fibrous connective tissue and substantial portions of flesh. Since primate morphology is ill-equipped to undertake such tasks (Van Valkenburgh and Wayne, 2010), stone tools were the only means by which hominins could efficiently do this (Shipman and Walker, 1989). Therefore, from at least 2.6 Mya, and likely earlier (Harmand et al., 2015), the hominin lineage is fundamentally linked to the acquisition and processing of food resources aided by lithic technology.

The arrival of Acheulean bifacial cutting tools (i.e. 'handaxes') at ~1.75 Mya (Lepre et al., 2011; Beyene et al., 2013; Diez-Martín et al., 2015) is suggested to indicate a further shift in reliance on the acquisition and processing of animal food resources. Faunal remains from the Acheulean identify the habitual exploitation of meat from a wide range of medium to large animals (Domínguez-Rodrigo et al., 2002; Pobiner et al., 2008). This includes evidence to suggest that hominins secured early access to carcasses, including those of mega-fauna, and were at times disarticulating elements for processing elsewhere (Pobiner et al., 2008; Pickering and Bunn, 2012; Domínguez-Rodrigo et al., 2014). Indeed, the association between handaxe technology and its suitability for substantial butchery behaviours/large carcass processing is pervasive in the literature (Jones, 1980, 1981, 1994; Toth, 1985; Schick and Clark, 2003; de Juana et al., 2010; Galán and Domínguez-Rodrigo, 2014; Key and Lycett, in press). There is then, evidence to suggest that post ~1.75 Mya hominins became more reliant upon the butchery of large mammals and the processing of substantial meat resources. Certainly, it is from this point that a number of morphological adaptations suggestive of increased meat consumption appear (McHenry, 1994; Aiello and Wheeler, 1995; Aiello and Wells, 2002; Antón, 2003; Milton, 2003; Bramble and Lieberman, 2004; Bunn, 2007; Antón et al., 2014). Outside of Africa and at later points in time there is further evidence that Acheulean technology was used in butchery activities (e.g., Shipman et al., 1981; Roberts and Partfitt, 1999; Bello et al., 2009; Yravedra et al., 2010), although this does not, of course, preclude handaxe use during plant processing as well (Domínguez-Rodrigo et al., 2001).

The recent discovery of a 1.42-million-year-old third metacarpal from West Turkana, Kenya, suggests that modern human-like hand anatomy is likely to have evolved in an Oldowan/early Acheulean behavioural context (Ward et al., 2014). Specifically, it identifies the earliest known appearance of a prominent styloid process, which is a morphological feature linked to the effective production and use of stone tools (Marzke and Marzke, 1987; Napier, 1993; Marzke, 1997, 2013; Kivell, 2015). A similar date for the emergence of more modern human-like hand anatomy is further supported by a proximal hand phalanx, dating to 1.2–1.3 Mya from Atapuerca (Spain), which exhibits similar morphological features to later Homo (Lorenzo et al., 2015), and a 1.8 Mya proximal phalanx from Olduvai Gorge indicating the presence of modern human-like manual dimensions (Domínguez-Rodrigo et al., 2015). Earlier fossil evidence indicates the transitional nature of some australopithecine species, both in terms of manual anatomy and manipulative capabilities (Tocheri et al., 2008; Kivell et al., 2011; Rolian and Gordon, 2013). There is, however, a distinct lack of remains from early members of the genus Homo and, as such, the relative speed with which hand anatomy evolved during the Oldowan/early Acheulean is unclear.

Subsequently, much of what is known about the selective pressures experienced by the hominin hand during this period has been derived from experimental investigations into stone tool production and use with modern human referents (e.g., Marzke and Shackley, 1986; Hamrick et al., 1998; Marzke et al., 1998; Faisal et al., 2010; Key and Lycett, 2011; Rolian et al., 2011; Williams et al., 2012, 2014; Key and Dunmore, 2015). The primary aim of these investigations is the identification and comparison of relative recruitment indices and manipulative actions experienced between individual digits, muscles and joints in the upper limb. Essentially, they identify the anatomical features likely to have experienced selective pressures as a result of tool production/use. As recently reviewed by Marzke (2013), the thumb is likely to have been important in this context given its contribution to the manipulation of stone tools, hammerstones and stone cores. Indeed, in all of these tasks, the thumb is used to forcefully oppose the fingers when securing objects in the hand. Most pertinently, during flake tool use the thumb secures the flake against the distal or lateral aspects of the opposing fingers, while in handaxe use it secures it against the distal, medial and proximal aspects of a number of fingers (Marzke and Shackley, 1986; Marzke, 1997). As a result, features vital to the exertion and resistance of force through the thumb and fingers, including thumb size, digit robustness, thumb to finger length ratios, flexor pollicis longus development and trapezial joint surface areas, amongst others, are all traits considered key to the evolution of modern human manipulative capabilities (Napier, 1993; Marzke, 1997, 2013; Tocheri et al., 2008; Diogo et al., 2012; Almécija et al., 2015). Accordingly, individuals displaying increased measures in those traits are hypothesized to display increased capabilities and efficiency rates when utilising stone technology (Marzke, 2013; Kivell, 2015).

An increased ability to effectively and efficiently utilise stone cutting tools could have increased the relative importance of the role played by lithic technology within the subsistence strategies of hominins, and in turn, increased the frequency and importance of stone tool use and production within hominin populations. Relative to what is known about how stone tool related behaviours may have influenced the evolution of human hand anatomy, however, a great deal less has been empirically demonstrated in respect to how biometric variation may have impacted on technological choices and cultural variability in the Lower Palaeolithic. The notion that individual biometric differences significantly influence hand-held tool use or gripping tasks is, however, both long lived and widely supported within engineering and ergonomic literature (e.g., Tichauer and Gage, 1977; Hall, 1997; Ruiz-Ruiz et al., 2002; Edgren et al., 2004; Nicolay and Walker, 2005; Hwang et al., 2011), with it having been demonstrated on a number of occasions that optimal tool forms are directly related to the biometric traits of tool users (e.g., Eksioglu, 2004; Seo and Armstrong, 2008). Such considerations indicate that those tool forms that are of greatest functional value, and thus the tool forms most likely to be replicated, are determined by the biometric conditions observed in a tool user's upper limb. In other words, tool form is likely to be influenced by the physical properties of the tool user. Although researchers have similarly suggested links between hominin biometric variation/capabilities and the preferential production and use of variable stone tool forms/types (e.g., Marzke and Shackley, 1987; Niewoehner, 2001, 2006; Sandgathe, 2005; Gowlett, 2009, 2015; Lycett, 2013; Lycett and von Cramon-Taubadel, 2015; Key, 2016), direct evidence relating to these hypothesized relationships within Palaeolithic contexts is limited.

It is currently unknown whether or how a number of biometric traits associated with stone tool use display statistical correlations with functional efficiency, or concomitantly, if there are differences in the relative strength of correlation in the case of different tool types. This is despite the notion of co-evolutionary relationships between aspects of lithic technology and hominin upper limb anatomy being both reasonable and longstanding within the field (Washburn, 1959; Krantz, 1960; Napier, 1993; Marzke, 1997; Marzke and Marzke, 2000; Tocheri et al., 2008; Key and Lycett, 2011; Rolian et al., 2011; Kivell, 2015). Moreover, there has been little consideration of how the selective 'environment' of stone tool use might vary and interact differentially with physiological factors depending on the type of tool being used and the type of task being undertaken. Key and Lycett (In press) recently assessed the comparative effectiveness of flaked tools versus handaxes, using the same participants (n = 60) for each tool type. They did not, however, directly assess how biometric variation of participants affected performance of tools within these tool types. Hence, here we aim to more comprehensively analyse the extent to which individual biometric variation exhibits statistical relationships with functional efficiency in differing contexts of tool use and task type. Specifically, six key biometric parameters of the hand are investigated in terms of their relationship with tool-use efficiency in both flake cutting tools and handaxes, over extended periods of use and multiple types of cutting task.

2. Materials and Method

2.1 Experimental Procedures

A total of 60 participants were selected to take part in the experiment from the student population at the University of Kent, Canterbury (UK). Prior to participation it was ensured that all participants had no experience using stone tools; this allowed the control of varying skill levels within the sample population. Biometric variation was ensured through the recruitment of both female and male participants (n = 38 and 22, respectively) with ages ranging between 18 and 56 years (mean = 26).

While a number of biometric traits have previously been suggested to be advantageous to the use of stone tools, here we record 'grip strength', 'pad-to-side pinch strength', 'tip-to-tip pinch strength', 'hand size', 'thumb length' and the ratio produced between the lengths of the thumb and index finger (hereafter referred to as '1D:2D ratio'). These represent a number of the key traits thought to influence the efficacy of stone tool use.

‘Grip strength’ was recorded using a hand dynamometer in a transverse hook grip (Figure 1). This is a test commonly used to compare the overall strength potential of individuals (Mathiowetz et al., 1985; Peters et al., 2011). ‘Pad-to-side’ pinch strength (also known as the ‘key pinch’) was recorded using a hydraulic pinch gauge, with the participant positioning the inferior surface of the ‘pinch point’ upon the joint of the proximal and intermediate second phalanges with the distal aspect of the thumb opposing the superior surface of the pinch point (Figure 1). ‘Tip-to-tip’ pinch strength was also recorded using the pinch gauge. In this instance, the participants pinched the distal aspects of the first and second distal phalanxes, with the first digit opposing from the superior surface of the pinch point, while the second digit opposed from the inferior surface (Figure 1). Both pinch measures are frequently used to record precision manipulative strength in the medical literature (e.g., Mathiowetz et al., 1985; Mullerpatan et al., 2013). The ability of humans to produce forceful precision grips, such as the ‘pad-to-side’ and ‘tip-to-tip’ pinch, is considered unique amongst primates and is widely reported as having been essential to the use of stone tools (e.g., Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke, 1997; Marzke et al., 2015). All three strength variables were recorded as the mean value of two repetitions at maximum exertion.

It is widely understood that the ability of modern humans to forcefully undertake both the ‘pad-to-side’ and ‘tip-to-tip’ pinch grips is in part due to the comparatively large, robust thumb that opposes the other four digits on the hand. Indeed, the relatively long thumb of modern humans (compared to, for example, *Pan*) facilitates the forceful manipulation of objects between the distal aspects of the thumb and both the distal and lateral aspects of the four fingers, and is widely considered to be associated with tool using/producing capabilities in fossil hominins (e.g., Alba et al., 2003; Tocheri et al., 2008; Kivell et al., 2011; Rolian and Gordon, 2013; Almécija and Alba, 2014). Subsequently, ‘thumb length’ and ‘1D:2D ratio’ are recorded here so as to assess the relationship between individual variation in this regard and tool-use efficiency. Multiple published methods exist with regards to the measurement of thumb length on experimental subjects (e.g., Voracek and Offenmüller, 2007; Jürimäe et al., 2008; Rolian et al., 2011). Here, using digital calipers, we use a ‘direct’ method (Kim and Cho, 2013), which records the distance between the distal tip of the thumb and the proximal palmer crease line at the thumbs intersection with the palm (Figure 1). To produce the 1D:2D ratio, a similar method was used to measure the index finger from its tip to the inferior crease line at its intersection with the hand (Figure 1). While the use of other digit measurement methods would alter the values identified for each individual (e.g., Kim and Cho, 2013; Xi et al., 2013), the fact that all participants were subject to the same procedures produced comparable data sets. Finally, ‘hand size’ was recorded in accordance with previous biometric research (Clerke et al., 2005; Key and Lycett, 2011) and measured the length of the supinated hand from the distal tip of the third digit to the first crease line at the wrist. Each variable was recorded prior to participants taking part in the experimental task. Descriptive statistics for the participants’ biometric variation can be seen in Table 1.

The experiment was designed in a manner that allowed the testing of multiple cutting tasks and durations with both handaxes and flake tools. The experimental assemblage consisted of 60 handaxes and 60 basic flake cutting tools made on flint and knapped by AJMK (Figure 2). Descriptive statistics for both tool type assemblages can be seen in Table 2. The handaxes include both pointed and ovate forms, along with examples that retain cortex on their proximal portion (Figure 2). The basic flake tools were similar in size to each other (i.e. coefficient of variation for ‘length’ is 13.1%) and all were above the efficiency threshold identified by Key and Lycett (2014) below which flakes are subject to markedly decreased cutting efficiency rates as a result of their diminutive size (i.e. below ~4.5 cm in length). Within each type of tool, all were assigned a number from 1 through to 60. Each participant was then randomly assigned both a flake and handaxe using a random number generator. The random number generator was also used to determine whether each participant used the flake or the handaxe first. Because each participant used one example of each tool type, this allowed direct comparisons of flake tools and handaxes within the same overall biometric context. A rest period of at least 10 minutes was provided between use of each tool type, which is adequate to allow muscular strength to recover such that fatigue was not a pertinent factor (Pitcher and Miles 1997; Key and Lycett, in press).

The task itself was comprised of three sections, each with a distinct type of material required to be cut. Each section was then further separated into six segments. Participants were required to sequentially undertake the first segment of each of the three materials and then repeat the task over, cutting the second segment of each material and so on until all six task segments of each material were completed. The three types of material were chosen to cover a variety of differing cutting conditions. While Lower Palaeolithic tools are thought to have primarily been tasked with cutting animal and plant materials, here we use industrially produced synthetic products that invoke a variety of similar cutting/deformation requirements (i.e. piercing, slicing, cleaving). While this does not directly replicate Lower Palaeolithic behaviours, it provides identical (i.e. consistently controlled) conditions for each participant, allows accurate and quantifiable task condition descriptions, and is easily replicable by others. Moreover, all tasks are intrinsically straightforward in nature and thus control for the effects of varying skill level that become more pervasive in tasks of increasing complexity, a problem identified in previous butchery experiments (Machin et al., 2007). As a result of these factors, our experimental protocol also allows for large, robust sample sizes to be collected. Notably, the use of materials similar to those used here has been extensively documented within engineering and ergonomic literature as accurately replicating the conditions of a number of biomaterials during hand-held cutting tool use (e.g., McGorry, 2001; Claudon and Marsot, 2006; Marsot et al., 2007; Gilchrist et al., 2008).

The first task station was comprised of two heavy-duty polythene bags (100 micron thick, 254 × 305 mm) filled with fresh potter’s clay, the latter of which was used simply to weight and secure the bags for cutting (see below). Both bags were then placed inside of a further heavy-duty polythene bag so that the polythene was double layered (Figure 3). Participants were required to cut along a dotted line that ran around the circumference of the outside of each bag (508 mm in length) with the condition that they must completely cut through both layers of polythene. There was no prerequisite for them to cut through the clay. Three dotted lines were drawn on each of the two bags with this producing the six segments of the first material section. This material did not require excessive levels of force or effort to cut through and was largely undertaken with a controlled slicing motion.

In contrast, the second task station provided a material that required greater effort to cut through. Specifically, participants were tasked with cutting through 30cm lengths of double layered, double walled corrugated cardboard (2 × 7.5mm thick, cardboard grade = 125). The cardboard was secured with metal bolts onto a wooden structure with beams on either side of the 30cm lengths (Figure 3). This not only provided support for the cardboard being cut (so that it did not bow under the pressure), but allowed the stone tool to pierce through the cardboard and go into an empty space. Participants were informed that they must cut fully through both layers of card for the entire 30cm length. Once again, there were six 30cm lengths on the cardboard and wooden structure with this forming the six segments of the second material.

The final task station required participants to cut through a 6mm thick piece of stranded natural fibre (hessian) rope that was secured to a wooden board (Figure 3). Each piece of rope was pulled taut and tied off on the underside of the board. Similar material has previously been used in experiments investigating the cutting efficiency of stone tools (Key and Lycett, 2011, in press) and provides a relatively small but resistant fibrous material that requires a precision cutting action. Six pieces of rope were tied to the board to form the six segments of this third and final material. Participants were instructed to completely sever the rope sections so that no fibre strands connect either portion of the material once cut.

Task efficiency was measured by the variable of ‘time taken’ recorded in seconds. This is a measure widely used in experimental analyses investigating stone tool efficiency and is known to be highly correlated to other efficiency measures such as the number of cutting strokes used (Jobson, 1986; Machin et al., 2007; Key and Lycett, 2014). ‘Time taken’ was logged from video recordings of each participant as they undertook the experiment, with the clock being started at the point of first contact between the stone tool and the material being cut and being stopped as it broke contact with the material on the final cutting stroke. If a participant paused to readjust the tool or material being cut, then this period of inaction was not included in the measurements of ‘time taken’. Each material segment was logged individually and as such the time taken for participants to move from one material type to another was not included. Participants were required to sequentially undertake the first segment of each of the three materials, before ‘restarting’ the task and cutting the second segment of each material. Essentially, the procedure was: cut first line on bags, cut first line on cardboard, cut first rope segment and then repeat. This was continued through all six segments and was implemented so that 1) the influence of task duration may be investigated over the six repetitions and 2) the experimental protocol controlled for any influence that fatiguing may have had on comparisons between material types.

2.2 Statistical Procedures and Analyses

The six biometric parameters under investigation here are all distinct manipulative traits discussed individually within the context of the evolution of modern human hand morphology. They are, however, also likely to be intercorrelated and display significant relationships between each other. Although a number of these traits are already known to be intercorrelated (e.g. Mathiowetz et al., 1985), it was necessary to understand the strength of any relationships for the present data set. Subsequently, the relationship between each biometric parameter utilised here was tested via a partial correlation coefficient. This gives a measure of the relationship between two variables while controlling for any covariance exerted by other variables. Statistically significant correlations were observed in accordance with Bonferroni correction and were only determined if $p \leq 0.002$.

Although the tasks utilised here are conceptually and practically straightforward (i.e. they require no specialised knowledge or skill), data from the first segment of each material (i.e. the first ‘run’) was not included in any of the following analyses so as to further control for the initial novelty of the task to novice participants. All analyses are then a product of the data from the final five segments of each material type.

Three sets of analyses were undertaken. The first aimed to understand the relative strength of relationship between each biometric variable and the functional effectiveness of each tool type, once covariance between variables is accounted for. Moreover, it tested whether or not a previously observed relationship between biometric variation and flake cutting efficiency (Key and Lycett, 2011) was similarly determined in handaxes. To accomplish this, the six biometric parameters under investigation were entered into a backwards stepwise regression against the total time taken to complete the whole task (segments 2 – 6 for all three task types). This was repeated independently for both tool types. This method of stepwise regression begins by placing all predictors (biometric variables) into the regression analyses and then calculates the contribution of each to the model’s prediction of tool efficiency. If a variable is not making a statistically significant contribution to the model’s prediction, then it is removed and the model is re-estimated for the remaining predictors. This is continued on a stepwise basis until only variables that make a significant contribution to the model’s prediction remain. This method of analysis allows the production of an ‘order of contribution’ detailing R^2 values, that in effect indicate the relative strength of relationship between each biometric variable and the functional efficiency measures (i.e. time taken) for each tool type. Stepping method criteria used an entry and removal value of 0.05 and 0.10, respectively.

The second set of analyses tested the prediction that the relationships observed between biometric variables and tool efficiency would be consistent throughout the duration of the task. Time data from the three corresponding task repetitions of each material type were combined to produce five distinct time variables relating to the order in which they were undertaken (e.g., the second segment from the polythene bag, cardboard and rope tasks were combined for each participant to form the first time variable). Backwards stepwise regressions were then run between the time values for these task repetitions and the six biometric parameters under investigation, for both flakes and handaxes. The null hypothesis being, that if task duration has no influence upon the strength of the relationships between biometric variation and tool efficiency then similar values should be returned across all five time variables.

The final set of analyses was designed to investigate whether the relationships observed across the whole task were consistent when the data was split into the individual tasks (i.e. material types). To assess this, the time taken from all five segments of each material type was combined. Backwards stepwise regressions were then run between the six biometric parameters and the combined time data for each of the tasks, for each of the stone tool types. If task type has no effect upon the relationships between biometric parameters and stone tool efficiency, similar values should be returned across all task types.

3. Results

As expected, the partial correlation coefficient tests identified significant correlations between several biometric traits (Table 3). This confirmed correlations between hand and thumb size (p = 0.0001), grip and pad-to-side pinch strength (p = 0.0001), and hand/thumb size and 1D:2D ratio (p = 0.0001 in each instance). Although non-significant after Bonferroni correction was applied, it also indicated a relationship between the two pinch strength measures (p = 0.005). No significant correlations were identified between strength and size/ratio variables. Indeed, it appears that within the given range of variation present in the current data set, hand size, thumb length and digit ratios are not significantly related to manipulative strength potential, once covariance between variables is controlled for (Table 3).

The first set of backwards stepwise regressions were undertaken to determine whether the efficiency of both flakes and handaxes were significantly related to the biometric variation of tool users, and what the relative strength of each relationship was once covariance had been accounted for. Results identified that both tool types were significantly related to tool user biometric variation. ‘Grip strength’ was determined to be the most significantly important variable in the prediction of flake efficiency, with it explaining 22.8% of the variation observed (Table 4). This was followed by ‘tip-to-tip pinch strength’ which, although also a significant contributor to the final stepwise model, was only responsible for 4.2% of the variation observed (Table 4). The remaining four variables did not significantly contribute towards the final regression model with each explaining ≤ 3.3% of efficiency variation in their respective final models. ‘Hand size’ was determined to be the most significant predictor of handaxe efficiency rates, accounting for 32.6% of the variation observed (Table 4). The remaining five variables did not significantly contribute to predictions of handaxe efficiency with each explaining ≤ 2.5% of the variation observed in the final models in which they were included (Table 4). It therefore appears that at a general combined task level, grip strength is the most significant contributor to flake efficiency, while hand size is the most significant in relation to handaxe efficiency. It is, however, clear that for both flakes and handaxes, functional efficiency is significantly related to the biometric variation displayed by the tool users.

The second set of regressions tested whether the relationships observed between biometric variables and tool efficiency were consistent across extended durations of tool use. The uniformity of flake significance values across all five task repetitions was very high (Table 5). For all of the five task repetitions, 'grip strength' was determined by stepwise regression to be the most significant predictor of flake efficiency. 'Tip-to-tip pinch strength' appears to be the next most significant predictor, regularly being listed as second in the order of contribution; moreover it was on two occasions a significant contributor to the final stepwise model. Conversely, 'hand size', 'thumb length' and 'pad-to-side' pinch strength appear to be largely ineffectual in predicting flake tool efficiency.

In relation to handaxe efficiency, 'hand size' was consistently returned as the most significant predictor of handaxe efficiency rates (Table 5). Similarly, 'grip strength' was consistently the second most important variable. 'Thumb length', 'pad-to-side pinch strength', and '1D:2D ratio' are consistently identified by the stepwise regression as being relatively poor predictors of handaxe efficiency. In sum, it appears that across extended periods of tool use (mean total time = 252.3 and 298.8 seconds for flakes and handaxes, respectively) the relationships observed between biometric parameters and tool use efficiency remain consistent.

The final set of results aimed to identify whether the relationships observed between biometric variables and tool efficiency were consistent across the different types of cutting activity. Results indicated that there is some relationship between task types and which of the biometric traits are of greatest influence to efficiency rates (Table 6). Specifically, there appear to be distinctions caused by the relative force and precision required by cutting tasks. Indeed, for flake tools it appears that in the rope cutting task grip strength was not of significant consequence to flake cutting efficiency and was the first variable removed by the stepwise regression (Table 6). This is in contrast to the other two tasks, where grip strength is not only significantly related to flake efficiency, but is identified as being the most significant contributing variables in both instances (Table 6). Thumb length also appears to be of significant consequence to flake efficiency and is identified by stepwise regression as being the first and second significant variable during the rope and polythene bag cutting tasks, respectively. It is, however, identified as the weakest predictor of efficiency in the cardboard cutting task (Table 6).

Similarly to flake tools, ‘grip strength’ is identified as being of importance in all three handaxe tasks; however, it is only the most significant variable in the cardboard task, and is second in the other two tasks to ‘hand length’. Indeed, ‘hand length’ is the most significant predictor of handaxe cutting efficiency in the other two tasks, and yet for the cardboard tasks it is determined to be of little importance. ‘1D:2D ratio’, ‘tip-to-tip pinch strength’ and ‘pad-to-side pinch strength’ appear not to be significant predictors of handaxe efficiency rates in any of the tasks.

Overall, results identify some uniformity with regards to the relationships between biometric variables and tool efficiency across the different types of cutting task. There are, however, exceptions, and this appears to link strength variables as being of increased importance when cutting large, resistant portions of material, and hand dimensions as being of increased importance when undertaking small tasks requiring a degree of precision.

4. Discussion

The ability to efficiently use stone tools has long been suggested as a key selective pressure in the evolutionary history of the hominin hand (e.g., Washburn, 1959). A basic prediction of this hypothesis is that biometric variation of tool users displays a statistical relationship with cutting efficiency in simple cutting tasks. Recently this was supported experimentally when it was shown that an individual’s grip strength and hand size is significantly related to the efficiency and force with which flake tools can be used (Key and Lycett, 2011; Key, 2013). In other words, it was demonstrated that biometric variation at a general level is indeed a pertinent variable in terms of effective stone tool use, and therefore, could have been subject to selection if such tool use was ultimately linked to biological fitness, as is likely in a subsistence related technology (Shipman and Walker, 1989; Marzke 2013). A relationship between biometric variation and differing tool use capabilities is, of course, inevitably at the core of any hypothesis that posits a link between evolutionary advantage in a Lower Palaeolithic behavioural context and resultant, observable patterns of adaptive morphological change in the fossil record (see e.g., Rolian et al., 2011; Williams et al., 2012;

Key and Dunmore, 2015). Here, it has been shown that the hypothesized selective factors may be dependent on a number of different contextual factors. In general terms, significant relationships have been observed between biometric parameters and stone tool efficiency across extended periods of tool use, multiple types of cutting tasks, and both flake tools and handaxes. This would support the basic contention that biometric variation in populations of hominin tool users might have provided a target for selective factors associated with such patterns of tool use; in turn, resulting in the observable patterns of change in human hand anatomy recorded in the fossil record. At a more detailed level our results do, however, identify distinctions between a biometric parameter's relationship with stone tool efficiency dependent upon the type of tool being used, and the type of task being undertaken. As discussed below, these results suggest several distinct sets of implications.

4.1 The influence exerted by tool use context

The finding that biometric variation in individual tool users is correlated with efficiency in the case of both flakes and handaxes implies that putative selective pressures can no longer necessarily be focused solely on the Oldowan or the recently described 'Lomekwian' (Harmand et al., 2015). Rather, over two million years of stone tool use could potentially have been selecting for derived human anatomical traits in the hand, including in terms of stabilizing selection. Flake and handaxe use are, of course, not always mutually exclusive, nor does this suggest that continual anatomical modifications would be observed throughout this period. Rather, there is now evidence to suggest that throughout the habitual use of these two tool types, hominins were potentially subject to selective pressures favouring certain biometric conditions. This latter point is strengthened by the consistency of values across multiple cutting durations and material types. This indicates that under a variety of task conditions, hominins displaying certain biometric conditions would likely have been undertaking cutting tasks more efficiently than others.

Specifically with regards to the influence of task duration, it has been demonstrated that over relatively long periods of tool use, the significance of these relationships is consistent for both flakes and handaxes. Essentially, the relative strength of the efficiency disparity between participants remained the same irrespective of what point during a cutting task relationships were recorded. While the analyses presented here detail only the strength of relationships for cutting activities of ~ 5 minutes (on average), it could be hypothesised that the relative strength of relationships will remain constant in durations beyond this. That is, while individuals may become fatigued and returns will diminish accordingly, the strength of the divergence in efficiency between individuals of varying biometric levels would remain constant; essentially all individuals would fatigue at a similar rate. Ergonomic data supports such a statement as grip strength and manipulative fatiguing rates have been shown to be unrelated (Nicolay and Walker, 2005). This is of importance as tool use durations can be highly variable and largely depend upon carcass/plant material size, completeness, skill level and the specific tasks being undertaken (disarticulation, skinning etc.) (Lupo, 1998; Machin et al., 2007; Haynes and Klimowicz, 2014). Hence, according to the results reported here, irrespective of whether hominins were engaged in relatively brief cutting activities on scavenged carcasses, or the extended butchery of whole carcasses, efficiency rates will vary dependent upon individual biometric variation. The fact that this is supported for both flakes and handaxes is consistent with ergonomic literature detailing that fatiguing rates of the flexor digitorum superficialis do not change as a function of grip span (Blackwell et al., 1999).

There do appear to be some distinctions between the observed relationships dependent upon the cutting task being undertaken, and the type of tool applied to the task. While the materials utilised here do not directly replicate Palaeolithic behaviours, a variety of cutting conditions/actions have been investigated, from which there appear to be distinctions caused by the relative amount of precision or force required to undertake the task. For relatively small flake tools there is a general emphasis on strength parameters being important during most cutting tasks. However, during the rope task (which requires greater cutting precision and the deformation of relatively little material), there is a stronger relationship with ‘thumb length’ and efficiency. This may be linked to the gripping of these not insignificantly sized flake tools (mean length = 6cm), with a longer thumb aiding manipulation and allowing greater precision when applying the cutting edge. Manipulative strength variables are then the second and third most important traits, although these are precision pinch strength measures as opposed to ‘grip strength’, thus further highlighting the emphasis on precision over gross force in this task.

For the relatively large handaxes (mean length = 14.8cm), it appears that larger hand dimensions are important to their use on tasks requiring some degree of accuracy (cutting the rope or following the line on the weighted bag). This is, however, of reduced importance when they are used to cut materials displaying greater resistance and requiring less precision (i.e. the cardboard cutting task). So, while a longer thumb is still important, ‘grip strength’ is most strongly predictive of efficiency in the cardboard task. This distinction is likely due to the greater size of handaxes, meaning that biometric variables influencing a person’s ability to control the tool are generally important, while those influencing the exertion of force are less so because there are factors (i.e. mass, momentum, surface area upon which to exert force) that naturally aide the exertion of force (Gowlett, 2006). This is particularly evident in the rope task, where tool control and the precise application of the cutting edge, as opposed to working force (i.e. loading), appear to be of greater importance (Key and Lycett, in press). Accordingly, this explains why ‘grip strength’ does not significantly contribute towards the final stepwise model, while in the other two task types it does.

Notably, Lower Palaeolithic cutting tasks are likely to have been variable, with a range of plant and animal materials potentially being required to be cut and deformed through stone tool use (e.g., Keeley and Toth, 1981; Domínguez-Rodrigo et al., 2001; Braun et al., 2010; Ferraro et al., 2013; Solodenko et al., 2015; Plummer and Bishop, 2016). Presented here is evidence to suggest that across such variation, task efficiency would have been significantly affected by individual biometric variability. Relationships with specific biometric traits would, however, have been both task and tool dependent. This is of potential importance to our understanding of early human tool use behaviours, particularly if the first (flaked) stone-tool use is considered to be undertaken by hominins displaying restricted precision manipulative force potential (e.g., Tocheri et al., 2003, 2008; Marzke, 2013; Rolian and Gordon, 2013; Kivell, 2015). Indeed, the reduced importance of manipulative strength potential during the cutting of relatively small material masses suggests that hominins displaying such traits may have been more favourably equipped for the processing of smaller material masses (e.g., scavenging meat scraps off carcasses) relative to larger, more resistant materials (e.g., whole carcasses). Certainly, it may have made removing meat scraps from a partially complete carcass a more favourable (and successful) task for early flake tool using hominins, relative to attempting to cut through tough hide and large masses of material on whole carcasses.

4.2 The contrasting influence of individual biometric parameters in differing tools types

The combined results from all stepwise regressions identify specific contrasts in relation to individual biometric parameters and predictability of the functional efficiency of Lower Palaeolithic stone tools. Notably, the strongest biometric predictor of flake tool efficiency is gross manipulative strength potential. Indeed, in all but one of the stepwise regressions ‘grip strength’ was identified as the most significant contributing variable to the prediction of flake efficiency rates. This supports previous research linking the evolution of forceful manipulative capabilities and effective flake tool use (Marzke, 1997; Key and Lycett, 2011; Rolian et al., 2011).

Both 'grip strength' and 'tip-to-tip pinch strength' were identified as stronger predictors of flake efficiency than 'pad-to-side pinch strength' in most instances. The potential significance of this is that the latter represents a measurement of the thumb's ability to exert manipulative force, while the former two are indicators of the ability of the fingers to resist and exert force. Thus, there appears to be a force-exertion role played by the fingers in the use of flake stone tools, and subsequently their strength is a more direct predictor of flake efficiency than is the case for pad-to-side strength, which is more heavily dependent on thumb strength. This is not to suggest the thumb is not heavily recruited, as numerous researchers detail that it is (see e.g., Marzke and Shackley, 1986; Marzke, 1997, 2013; Hamrick et al., 1998), nor does it suggest that the thumb does not exert more force than the fingers (Williams et al., 2012). Rather, there may also be a not inconsiderable force exertion role played by the fingers in respect to flake tool efficiency. This is most likely to be by the palmar surface of the second and third digits exerting force on the edge of the flake opposing the cutting edge, which in turn creates a 'downwards' momentum beneficial to cutting, and resists tool movement as it is drawn through or across a material (Figure 4). Indeed, this point has been similarly noted by Marzke and Shackley (1986), who identify that pad-to-side grips rarely occur during flake tool use and that the positioning of the index finger in opposition to the point of impact is important in tool control. This explains the importance of force exertion through the fingers while maintaining traditional gripping models that emphasise the flexion of the thumb against one aspect of the flake when securing it within the hand (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke, 1997, 2013; Hamrick et al., 1998). This does not, however, help explain the greater robusticity of the thumb relative to the fingers. It would be useful if future experiments were able to document the relative forces exerted by the fingers and thumb during flake tool use (c.f. Williams et al., 2012; Key and Dunmore, 2015). Such work may be able to assess whether the thumb requires greater force to secure flakes against the fingers, than the fingers do when contributing to pushing/resisting a flake as it is drawn through a material.

Another key result is that 'hand size' was consistently the most important biometric variable in the prediction of handaxe cutting efficiency. Hence, it appears that the efficient use of handaxes as a cutting tool is linked to the manual dimensions of the tool user, with increased hand sizes resulting in greater levels of cutting efficiency. It is, therefore, possible that the use of large cutting tools (such as large flakes and handaxes) may potentially have provided a selective pressure contributing towards the large manual dimensions seen in some later Homo species (e.g., Churchill, 2001; Ward et al., 2014; Lorenzo et al., 2015) relative to earlier Homo or australopithecines. Consideration of any evolutionary scenario must, however, be examined within an evolutionary context of increasing body sizes and changes observed in a suit of anatomical features that contribute to modern human-like manipulative capabilities. Accordingly, the precise role, if any, of large cutting technologies in the evolution of modern human-like manual dimensions in later Homo is unclear. Nonetheless, it is evident from the results presented here that individuals displaying increased measures in this regard would likely exhibit greater efficiency rates for handaxe use, and thus have an advantage over their smaller handed counterparts, at least within behavioural contexts requiring the use of large cutting tools. Hence, Homo species with relatively large manual dimensions (i.e. after ~1.8-1.4 Mya [Ward et al., 2014; Domínguez-Rodrigo et al., 2015]) may have found the use of handaxes and other large cutting tools to be a more worthwhile endeavour than other recent, but more diminutive, hominin species (e.g. Larson et al., 2009). This is not surprising as the ability to exert force upon a tool, and thus comfortably grip, manipulate, and resist a tool, has been previously linked to an individual's manual dimensions, with optimal tool sizes altering in line with tool-user hand size (Eksioglu, 2004; Figure 5).

A further possibility is that the onset of the Acheulean techno-complex was, a priori, dependent upon hominins displaying relatively large hand sizes, at least relative to the hominin species producing Oldowan stone tools (the Acheulean's immediate technological precursor). Indeed, for handaxes to have been adopted as an efficient means to cut and deform material in the first instance, it must have required the tool users to have been effectively able to utilise them (Crompton and Gowlett, 1993; Kempe et al., 2012) and our results indicate that hand size is pertinent in this respect. This is not to conclude that the onset of the Acheulean is an indicator of modern human-like hand anatomy. Rather, it is possible to state that hominins would likely have displayed manual dimensions that were increased relative to those required purely for 'typical' Oldowan flake tool use, and that these dimensions are likely to be nearer the modern human range. Recent discoveries of fossils and handaxes are broadly supportive of such a statement, indicating that the emergence of both this new tool type and novel anatomical condition may have been broadly coincident (Beyene et al., 2013; Ward et al., 2014; Domínguez-Rodrigo et al., 2015; Diez-Martín et al., 2015; Lorenzo et al., 2015). This is particularly noteworthy since our results show that individuals with smaller hands may have more profitably employed the use of flakes as opposed to handaxes. Indeed, within the 20 smallest handed individuals in the present sample, Mann-Whitney U tests identified that it was significantly more efficient for them to utilise flakes in all three task conditions than it was for them to use handaxes (p = 0.0001, in each instance). While future experiments are necessary (e.g., Eksioglu, 2004), both this and the main experimental results support the hypothesis that the origin of the Acheulean may be linked to relatively large, relatively more human-like, hands. Thus, the onset of the Acheulean was likely not only dependent upon relevant cognitive abilities (e.g. Stout et al., 2008; Faisal et al., 2010; Stout, 2011), and social learning factors (Lycett et al., 2016), but physical factors may also additionally have curtailed the use and adoption of handaxe technology up until a specific point in human evolutionary history.

The finding that 1D:2D digit ratio does not significantly predict the efficiency with which either flakes or handaxes can be used may also be of importance. Indeed, our results suggest that hominins with modern human thumb-to-finger-length ratios would not have been subject to evolutionary pressure selecting for an alteration to this ratio as a result of stone tool use. This does not imply that the length of the thumb relative to that of the fingers, and thus the ease with which their distal tips may oppose, is not of consequence to the use of stone tools. Indeed, numerous publications note that flake tools are manipulated between the distal aspects of the thumb and distal/lateral aspects of the opposing fingers (Marzke and Shackley, 1986; Marzke, 1997), with an increased ability to strongly oppose the fingers with the thumb widely being reported as indicative of increased tool-use capabilities in hominins (e.g. Napier, 1993; Marzke, 1997, 2013; Rolian et al., 2011). Rather, it suggests that the range of variation present within modern humans is not enough to induce a significant effect on tool efficiency rates. Indeed, Almécija et al. (2015) have recently argued that humans likely display only slightly modified finger and thumb length proportions (i.e. inter-digit ratios) since our last common ancestor with Pan. In relation to this, it should be noted that the results discussed here have been produced by individuals with modern human upper limb anatomy and are, therefore, of most relevance to species that similarly display the suit of anatomical features contributing to our unique manipulative repertoire. Hence, while the implications discussed here are important for understanding tool use capabilities in hominin species with modern human-like and transitional hand anatomy, inferences may be more limited for species displaying marked arboreal adaptations.

5. Conclusion

Presented here is evidence to suggest that the efficiency with which stone flakes and handaxes were used by Lower Palaeolithic hominins was significantly related to individual biometric variation. Specifically, it has been demonstrated that manipulative strength is the strongest predictor of efficiency during the use of flake tools, and hand size is the strongest predictor of handaxe efficiency. Furthermore, these relationships are demonstrated to be consistent across extended periods of tool use. Relationship differences are, however, identified between biometric variables and tool efficiency dependent upon the conditions of the task being undertaken, and whether individuals are using flakes or handaxes. So, although there are significant relationships with biometric traits in all instances, the specific relationship that each trait has with task efficiency is dependent upon task conditions and tool choice. It is, therefore, likely that no matter the type of cutting task being undertaken, Lower Palaeolithic hominins would have displayed disparate efficiency rates dependent upon individual levels of biometric variation. As a result, individuals displaying greater measures in these traits will have displayed more efficient tool use behaviours, in turn having an evolutionary advantage within a Lower Palaeolithic behavioural context. Indeed, effective use of handaxes as cutting tools depends heavily on specific biometric conditions as an anatomical prerequisite. Hence, the onset of the Acheulean may have been dependent, a priori, on the presence of hand dimensions that are closer to those of modern humans than are typically displayed by earlier hominins such as the australopithecines.

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Figures

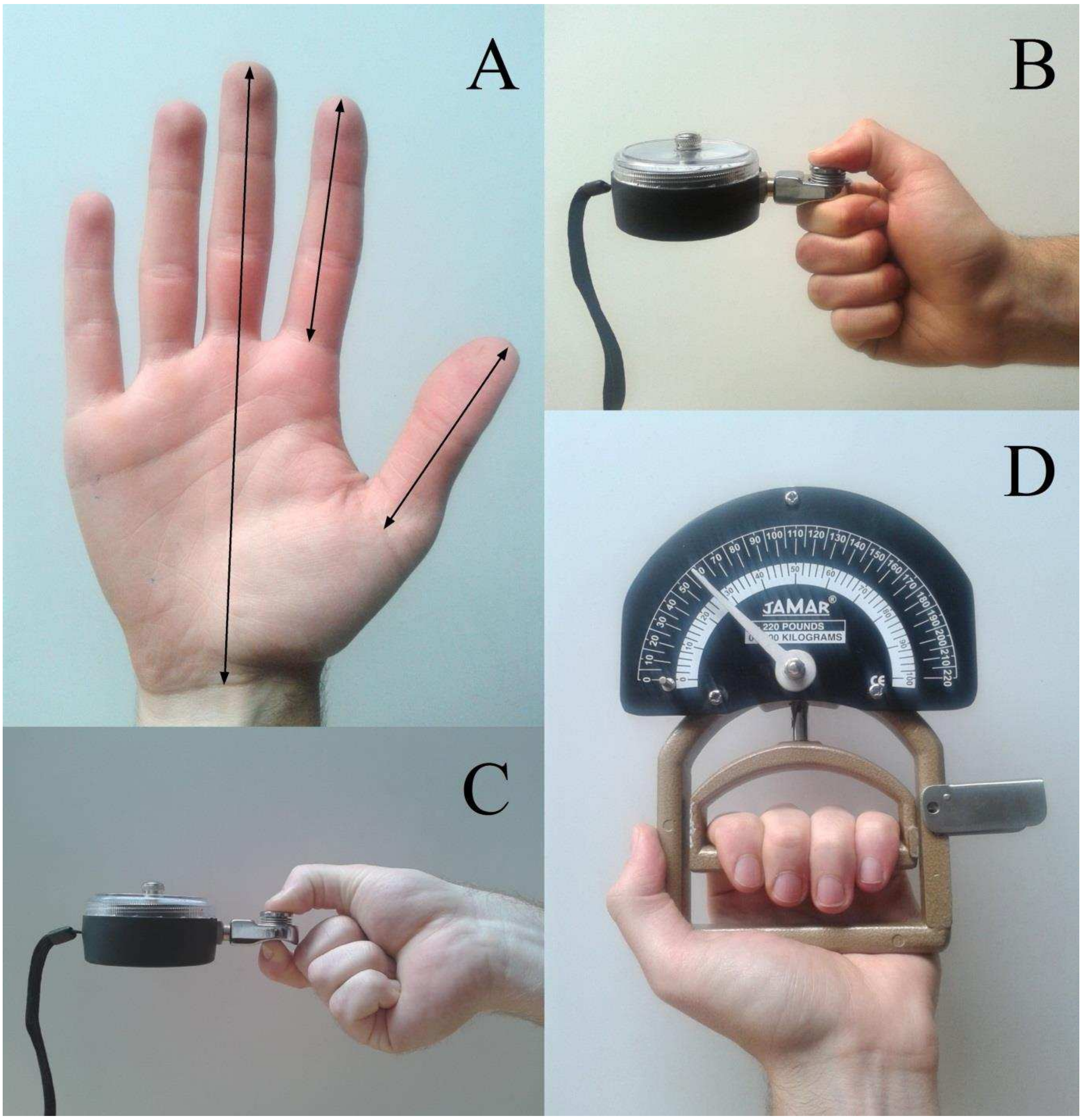

Figure 1. Equipment and methods utilised to obtain the biometric parameters investigated for each participant; namely, a) Thumb Length, Hand Size, and 1D:2D Ratio, b) Pad-to-Side Pinch Strength, c) Tip-to-Tip Pinch Strength, and d) Grip Strength.

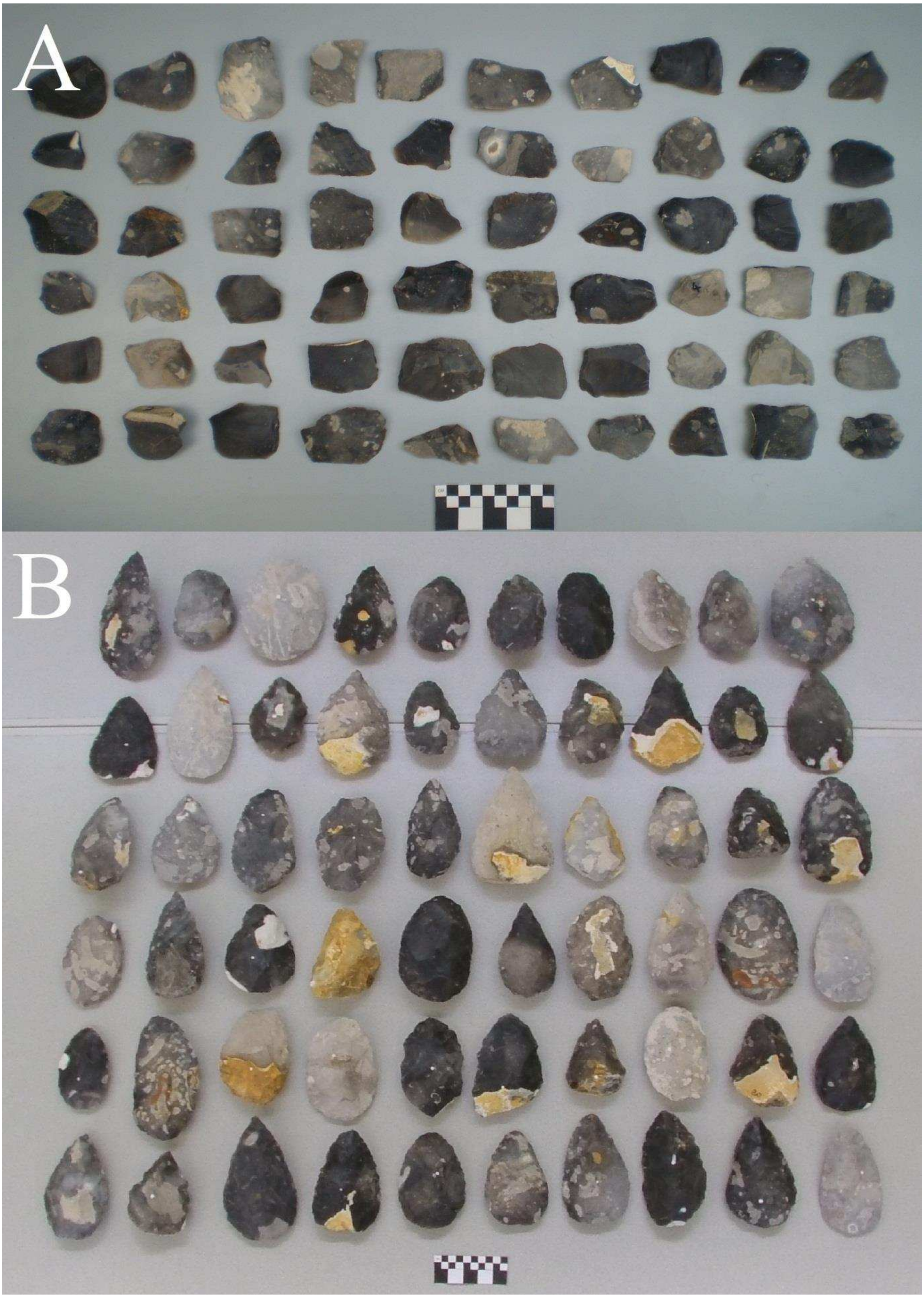

Figure 2. The 60 flakes (a) and 60 handaxes (b) utilised in the present experiment. Scale bar = 10 cm in both images.

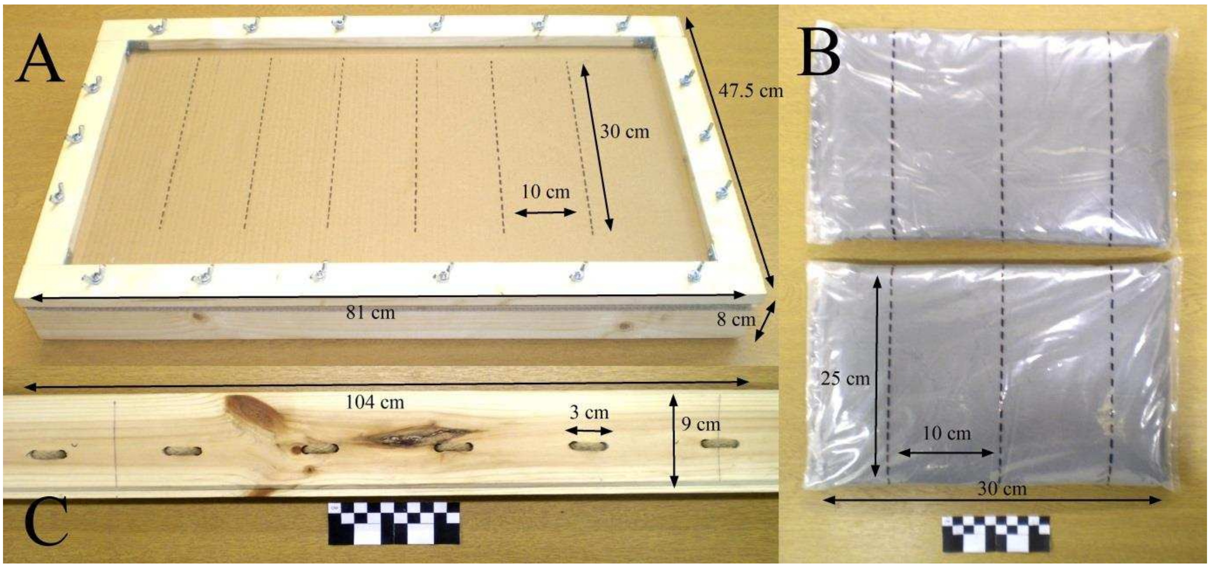

Figure 3. The cutting tasks undertaken by each participant, including; a) the double layered cardboard, b) the polythene bags filled with clay and c) the natural fibre rope. Note the six segments in each instance.

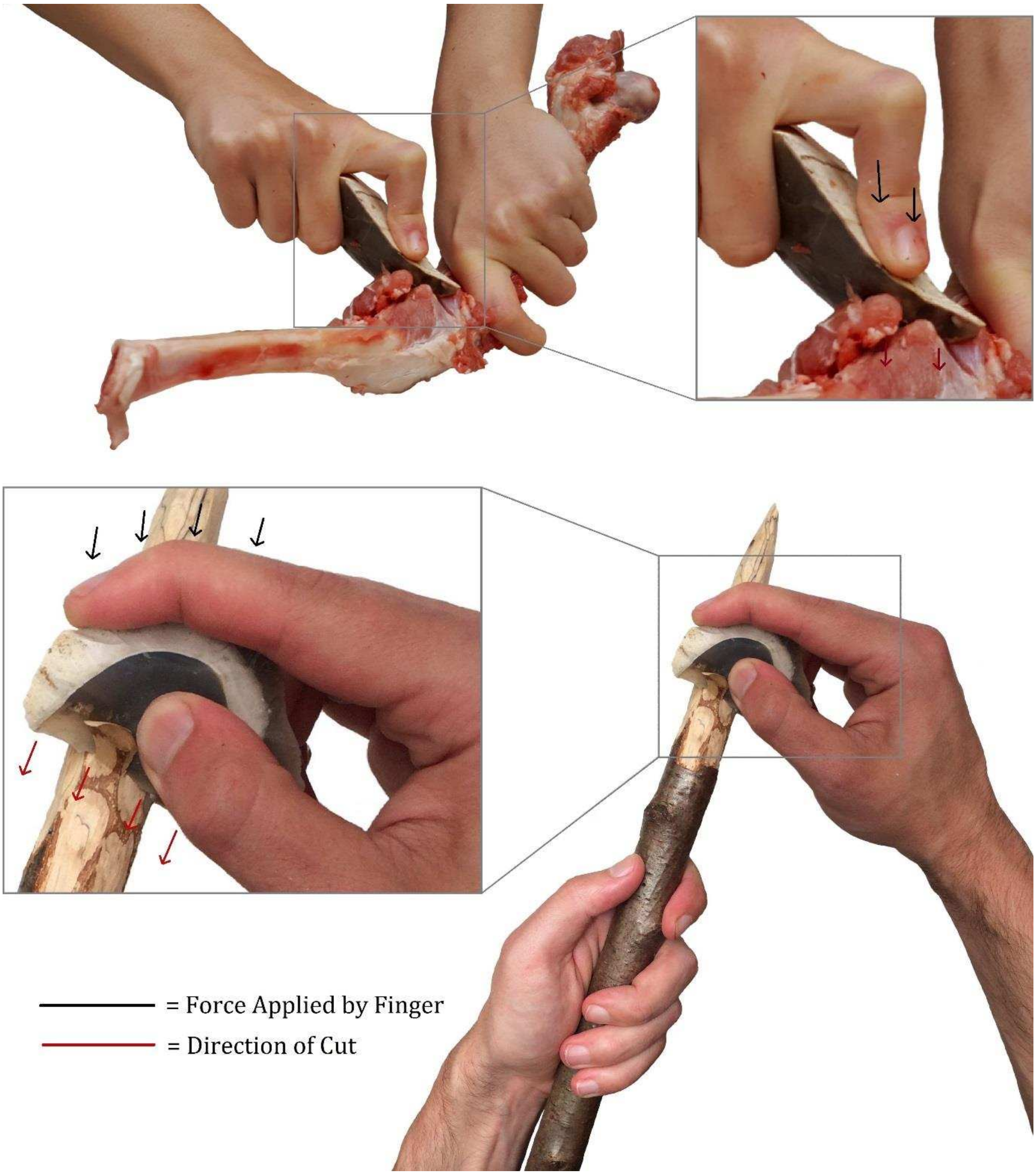

Figure 4. Images illustrating the force exertion role played by the fingers during flake tool use. This force exertion role is predominantly undertaken by the index finger, although the middle finger can similarly be recruited during the use of larger tools.

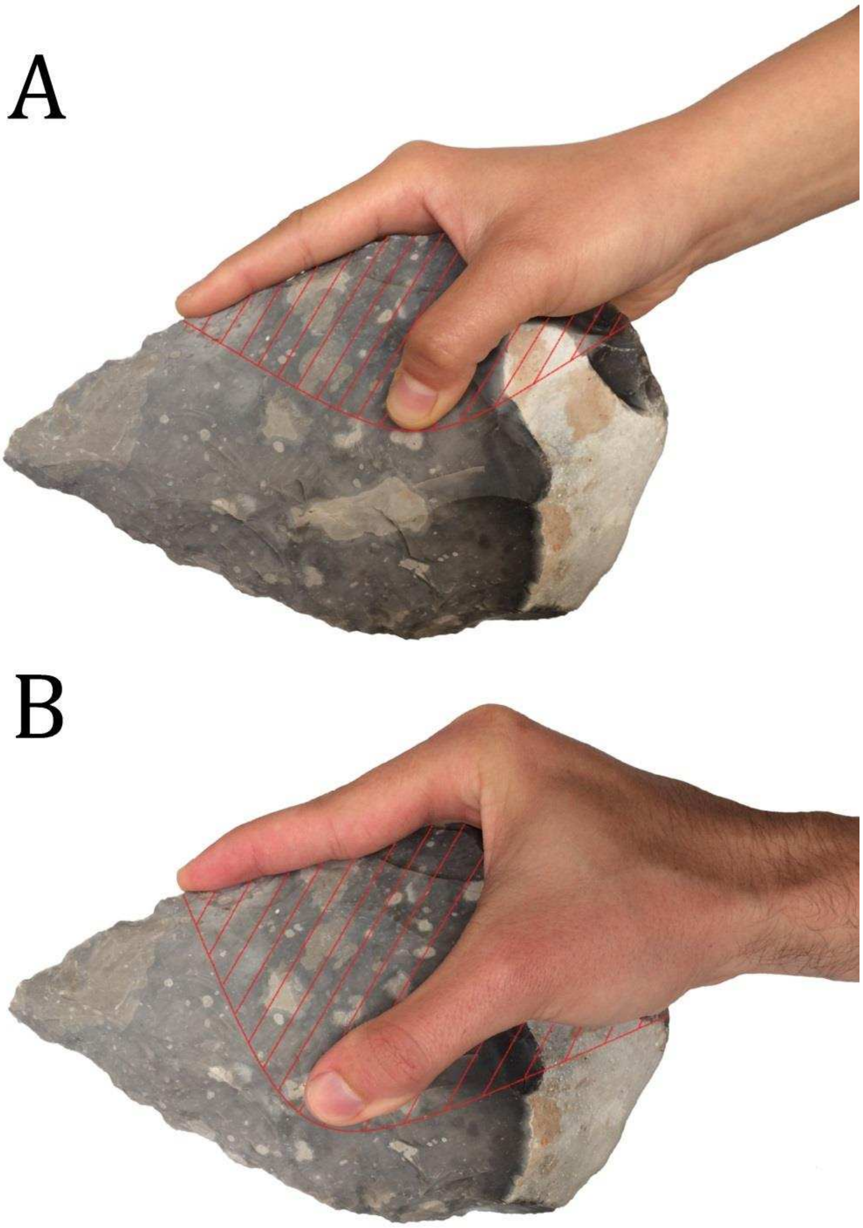

Figure 5. The relative capacity of individuals with differing hand sizes to effectively manipulate and utilise a handaxe. Identified within figures A and B are the proportion of the handaxe's mass that can be forcefully opposed between the fingers and thumb of two individuals with hand lengths of 171mm and 201mm (respectively). These reflect differences in the amount of material/mass located within an individual's grip and ultimately their ability to control and exert forces on aspects of the handaxe located furthest from point of contact with the palm.

Tables

Table 1. Descriptive statistics for each biometric variable under investigation here (n = 60).

	Thumb Length (mm)	Hand Size (mm)	Grip Strength (Kgs)	Pad-to-Side Pinch Strength (Kgs)	Tip-to-Tip Pinch Strength (Kgs)	1D:2D Ratio
Mean	66.5	181.1	38.4	7.8	4.9	0.938
Range	53.1 - 81	147 - 209	22 - 70	4.9 – 13.7	2.3 – 9.6	0.828 – 1.041
Standard Deviation	5.8	13.7	11.1	2	1.7	0.042

Table 2. Descriptive morphological statistics for the flake and handaxe assemblages utilised (n = 60 in each instance).

	Flakes				Handaxes			
	Length (mm)	Width (mm)	Thickness (mm)	Mass (g)	Length (mm)	Width (mm)	Thickness (mm)	Mass (g)
Mean	59.7	45.7	13.8	34	148	100.7	41.3	598
Range	45.5 - 75	29.8 – 68.7	4.2 – 35.5	10.7 – 84.5	112.2 – 205.5	75.8 - 141	25.2 – 66.7	257 - 1953
Standard Deviation	7.8	6.9	5.2	15.7	20.2	14.4	10.2	294.7

Table 3. Partial correlation coefficient tests between the six biometric parameters under investigation (n = 60). In each correlation, the other four variables have been held constant. Significant values are determined in accordance with the Bonferroni correction and are indicated in bold if p ≤ 0.002.

	Thumb Length		Hand Size		Grip Strength		Pad-to-Side Pinch Strength		Tip-to-Tip Pinch Strength	
	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient	p	Coefficient
Thumb Length	-	-	-	-	-	-	-	-	-	-
Hand Size	**.0001**	.866	-	-	-	-	-	-	-	-
Grip Strength	.737	-.046	.085	.232	-	-	-	-	-	-
Pad-to-Side Pinch Strength	.728	-.048	.648	.062	**.0001**	.620	-	-	-	-
Tip-to-Tip Pinch Strength	.678	.057	.793	-.036	.128	.206	.005	.373	-	-
1D:2D Ratio	**.0001**	.705	**.0001**	-.689	.037	.280	.623	-.067	.787	-.037

Table 4. The results of backwards stepwise regression tests between the six biometric parameters under investigation here and the combined ‘time taken’ values from the flakes and handaxes over the course of the second – sixth task segments across all material types (n = 60). Indicated R^2 values are taken from the change in model R^2 values. Model R^2 values are displayed on a step-by-step model basis and are inclusive of all predictors within that model. In all stages of the model significance values are below 0.05.

Order of Contribution to Tool Efficiency	Flakes				Handaxes			
	Model	Predictor	R^2	Model R^2	Model	Predictor	R^2	Model R^2
1	5	Grip Strength	.228	.228	6	Hand Size	.326	.326
2	5	Tip-to-Tip Pinch Strength	.042	.269	5	Grip Strength	.025	.351
3	4	1D:2D	.033	.302	4	Tip-to-Tip Pinch Strength	.002	.353
4	3	Hand Size	.008	.310	3	1D:2D	.001	.354
5	2	Thumb Length	.0001	.311	2	Pad-to-Side Pinch Strength	.0001	.354
6	1	Pad-to-Side Pinch Strength	.0001	.311	1	Thumb Length	.0001	.354

Table 5. Backwards stepwise regressions run to identify whether the relationships observed between biometric variables and tool efficiency are consistent across extended task durations. The six biometric parameters under investigation here and the ‘time taken’ values for both flakes and handaxes from the three corresponding segments from each material type across repetitions two – six are compared (n = 60). As per the methods in section 2.2 and table 4, the order of contribution to tool efficiency rates have been calculated via backwards stepwise regression as an indicator of actual influence by variables once covariance has been accounted for. In all stages of the model significance values are below 0.05.

Flakes															
	2			3			4			5			6		
Order of Contribution	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2
1	6	Grip Strength	.162	5	Grip Strength	.268	6	Grip Strength	.187	5	Grip Strength	.199	5	Grip Strength	.154
2	5	Thumb Length	.031	5	Tip-to-Tip Pinch Strength	.067	5	Tip-to-Tip Pinch Strength	.037	5	Tip-to-Tip Pinch Strength	.025	5	1D:2D Ratio	.102
3	4	Tip-to-Tip Pinch Strength	.025	4	1D:2D Ratio	.021	4	Thumb Length	.013	4	1D:2D Ratio	.035	4	Tip-to-Tip Pinch Strength	.018
4	3	1D:2D Ratio	.008	3	Hand Length	.009	3	Hand Length	.007	3	Hand Length	.009	3	Hand Length	.011
5	2	Pad-to-Side Pinch Strength	.001	2	Pad-to-Side Pinch Strength	.003	2	Pad-to-Side Pinch Strength	.001	2	Thumb Length	.001	2	Thumb Length	.006
6	1	Hand Length	.0001	1	Thumb Length	.001	1	1D:2D Ratio	.0001	1	Pad-to-Side Pinch Strength	.001	1	Pad-to-Side Pinch Strength	.0001
Handaxes															
	2			3			4			5			6		
Order of Contribution	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2
1	6	Hand Length	.327	6	Hand Length	.284	6	Hand Length	.305	6	Hand Length	.329	6	Hand Length	.313
2	5	Grip Strength	.027	5	Grip Strength	.025	5	Grip Strength	.025	5	Grip Strength	.026	5	Grip Strength	.016
3	4	Tip-to-Tip Pinch Strength	.002	4	Pad-to-Side Pinch Strength	.000	4	Tip-to-Tip Pinch Strength	.005	4	Tip-to-Tip Pinch Strength	.005	4	Thumb Length	.002
4	3	1D:2D Ratio	.001	3	Tip-to-Tip Pinch Stren.001gth	.001	3	1D:2D Ratio	.003	3	1D:2D Ratio	.005	3	1D:2D Ratio	.005
5	2	Pad-to-Side Pinch Strength	.001	2	Thumb Length	.0001	2	Pad-to-Side Pinch Strength	.0001	2	Thumb Length	.0001	2	Tip-to-Tip Pinch Strength	.0001
6	1	Thumb Length	.0001	1	1D:2D Ratio	.0001	1	Thumb Length	.0001	1	Pad-to-Side Pinch Strength	.0001	1	Pad-to-Side Pinch Strength	.001

Table 6. Backwards stepwise regressions run to test whether the relationships observed between biometric variables were consistent across all task materials. The combined ‘time taken’ values for segments 2 – 6 in each material types were tested against each of the six biometric parameters under investigation (n = 60). As per the methods in section 2.2 and table 4, the order of contribution to tool efficiency rates have been calculated via backwards stepwise regression as an indicator of the influence exerted by variables once covariance has been considered.

Flakes									
	P. Bag			Cardboard			Rope		
Order of Contribution	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2
1	6	Grip Strength	.151	5	Grip Strength	.196	6	Thumb Length	.147
2	5	Thumb Length	.025	5	Tip-to-Tip Pinch Strength	.038	5	Pad-to-Side Pinch Strength	.011
3	4	1D:2D Ratio	.003	4	1D:2D Ratio	.022	4	Tip-to-Tip Pinch Strength	.015
4	3	Tip-to-Tip Pinch Strength	.001	3	Pad-to-Side Pinch Strength	.003	3	1D:2D Ratio	.012
5	2	Hand Length	.001	2	Hand Length	.002	2	Hand Length	.0001
6	1	Pad-to-Side Pinch Strength	.0001	1	Thumb Length	.0001	1	Grip Strength	.0001
Handaxes									
	P. Bag			Cardboard			Rope		
Order of Contribution	Model	Predictor	R^2	Model	Predictor	R^2	Model	Predictor	R^2
1	5	Hand Length	.283	5	Grip Strength	.389	6	Hand Length	.236
2	5	Grip Strength	.269	5	Thumb Length	.319	5	Grip Strength	.004
3	4	1D:2D Ratio	.004	4	1D:2D Ratio	.011	4	Tip-to-Tip Pinch Strength	.006
4	3	Thumb Length	.010	3	Tip-to-Tip Pinch Strength	.002	3	1D:2D Ratio	.0001
5	2	Tip-to-Tip Pinch Strength	.001	2	Hand Length	.001	2	Thumb Length	.002
6	1	Pad-to-Side Pinch Strength	.0001	1	Pad-to-Side Pinch Strength	.0001	1	Pad-to-Side Pinch Strength	.001