The Case Against Sexual Selection as an Explanation of Handaxe Morphology

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ABSTRACT

Many explanations have been put forward to account for the distinctive symmetrical teardrop shape of Acheulian handaxes but none is perhaps as controversial as the sexual selection hypothesis. In this paper, we outline the necessary assumptions and conditions underlying the argument for sexual selection as an explanation for handaxe morphology, critique this argument on the basis of the available evidence from comparative ethology, experimental psychology, and the archaeological record, and present several more parsimonious alternative explanations that are directly based on this available hard data.

INTRODUCTION

In two recent publications, Kohn and Mithen (1999; Mithen 2005) proposed an evocative and romantic theory explaining the morphology of Acheulian handaxes. This theory, meant to account for the abundance and remarkable elaboration of these artifacts, argues that the distinctive, symmetrical teardrop shape of Acheulian handaxes was the product of sexual selection. Their work has been cited in conference presentations (Machin and Hosfield 2006), academic publications (Buckley and Steele 2002; Dibble and McPherron 2006; Haselton and Miller 2006; Hopkinson and White 2005; Kuhn 2004; McNabb et al. 2004; Machin 2008; Machin et al. 2007; Rose 2006; Shennan 2002; White 2000; Wynn 2002), a recent textbook (Klein 2006) and in the popular press (McNeil 2006). With few exceptions (e.g., Marks et al. 2001; Shennan 2002; Whittaker and McCall 2001; see also Bolger 2006; Nowell 2000; Nowell and Chang 2008), this hypothesis is presented as if it were more than speculation. One exception is a short critique by Machin (2008), but in her paper she does not consider any of the relevant archaeological data, nor does she adequately evaluate Kohn and Mithen's hypothesis within the broader scope of the biological sciences.

In this paper, we outline the necessary assumptions and conditions underlying the argument for sexual selection as an explanation for handaxe morphology, critique this argument on the basis of the available evidence from comparative ethology, experimental psychology, and the archaeological record, and present more parsimonious alternative explanations that are directly based on hard data.

MODELS OF SEXUAL SELECTION

Sexual selection is a classic explanation in evolutionary ecology for conspicuous, sexually dimorphic traits in animals, and was considered a significant factor in evolution by Charles Darwin, who observed that animals in nature, across taxa, are often sexually dimorphic. Males are often "ornamented," while females are "unadorned" (Darwin 1871). Such dimorphism often is associated with reproductive behaviors.

In an evolutionary context, fitness is measured (in a gross way) by the proportional representation any individual has in successive generations—in other words, how many of its alleles it passes on via its offspring. Sexual selection is selection that results in differential mating success. This general definition may apply to males or females. However, because males and females experience different costs with respect to reproduction (Bateman 1948), they employ different "investment strategies"—typically, males (the lower-investing sex) compete for mating opportunities (intrasexual selection); and females, who bear the brunt in terms of mating "mistakes," make mating decisions on the basis of some observable, variable phenotypic character of the other sex (intersexual selection) (Clutton-Brock and Vincent 1991; Trivers 1974).

While models, and examples, of intrasexual selection (male competition) are relatively straightforward, models of intersexual selection (female choice) have generated more controversy. Ecologists and evolutionary biologists have formulated a number of theoretical models implicating various mechanisms by which choosy females discriminate among males, and by which male traits and female preferences may then evolve (Andersson and Simmons 2006). Females may make choices resulting in *direct benefits* in terms of things like food resources or paternal care provided by a male. Females also may receive *indirect benefits* if the males they mate with pass on heritable variation that confers increased fitness upon their offspring in terms of either increased viability or enhanced attractiveness. Or, they may simply have a sensory bias that evolved in a context other than sexual selection. These mechanisms are not mutually exclusive, and may operate together or as a continuum in any given situation (Kokko 2003). These models draw from organismal biology, evolutionary theory, population genetics, and more recently, molecular genetics and functional genomics.

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Such models constitute testable hypotheses that are typically addressed using real data collected by observing populations of living animals. There is a long tradition of such studies, which began to flourish about 20 years ago, and grow more sophisticated with each passing year. That females make mating decisions on the basis of male phenotype has been verified through both field and experimental studies. For example, female long-tailed widowbirds (*Euplectes progne*) prefer males with longer tails, and their preferences can be manipulated by artificially shortening or elongating male widowbird tails (Andersson 1982). Another classic example of empirical studies in sexual selection involves peafowl (genus *Pavo*), highly sexually dimorphic birds that exhibit lekking behavior, meaning that males gather in a common area to display to females, which then choose among them for mating opportunities.

Petrie and colleagues conducted a series of observational and experimental studies in a feral population of blue peafowl (*Pavo cristatus*), examining the role of the peacock's elaborate train in peahen choice and peacock reproductive success (Petrie 1994; Petrie and Halliday 1994). They observed that peacocks sporting the largest trains, with the most eyespots, were the most successful males on the lek. They experimentally manipulated the trains of peacocks by removing eyespots, and showed that males with missing eyespots suffered a significant decline in mating success between seasons compared to a control group. Having demonstrated that peahens take train morphology into account when making mating decisions, they then conducted a controlled breeding experiment to determine whether or not the females were gaining any indirect genetic benefits for their offspring by being choosy. Peacocks with more elaborate trains sired larger offspring (regardless of hen quality) that grew faster and demonstrated significantly higher survivorship at one year of age.

These findings were consistent with what are known as "*indicator*" models of intersexual selection based on indirect benefits to the female. In these models, the relationship between expression of a male trait and male quality is such that the trait constitutes an "honest" advertisement, often because it is costly (a "handicap") and only higher-quality males can afford to express it. Indicator models require that the male trait is associated with heritable fitness. Females benefit from their choices by producing offspring that are at a selective advantage in the environment (Trivers 1972; Zahavi 1975, 1977; Zahavi and Zahavi 1997).

Models of sexual selection in living organisms intended to explain the evolution of dimorphic traits involve conditions and assumptions that are amenable to empirical testing. These can include, but are not limited to:

1. observation of female preference for the male trait;
2. association between a male trait and male viability;
3. association between a male trait and the fitness of his offspring, as observed through multigenerational field or laboratory studies;
4. phylogenetic evidence for the time of origin of a male trait; and,
5. genetic studies discovering gene(s) correlated with variation in male traits, and demonstrating linkage to gene(s) correlated with female preference.

In this context, we may in turn evaluate Kohn's and Mithen's (1999) hypothesis.

THE SCENARIO: SEXUAL SELECTION AND HANDAXE MORPHOLOGY

In their 1999 article, Kohn and Mithen posed "five fundamental questions" that a theory of handaxe morphology needs to answer. These questions are:

1. Why are handaxes so pervasive in the archaeological record?
2. Why are they often found in such prolific numbers at individual sites?
3. Why was time invested in making handaxes, when simpler tools would suffice for cutting purposes?
4. What was the value of imposing such high degrees of symmetry in handaxe manufacture?
5. How can one explain handaxe oddities, such as giant handaxes or other "dramatic objects?"

Kohn and Mithen (1999; Mithen 2005) allege that *Homo erectus* (sensu latu) males made handaxes primarily to attract females for mating purposes. According to this scenario, handaxe shape serves as an indicator of the knapper's knowledge of where good raw material can be found, his ability to execute a plan, his good health, and his social awareness. Mithen argues that this is why handaxes often are found with little or no evidence of wear, as "once made they were of limited further use" (2005: 191), and were therefore simply thrown away. Variability in handaxe morphology also is explained under this model—males are presumed to have made highly symmetrical handaxes, with females responsible for less refined tools (Kohn and Mithen 1999: 523). In this argument, the phenotypic trait of interest (or the peacock's train) is the morphology of handaxes produced by a particular male. The variation in the trait that is allegedly governed by sexual selection (or the number of eyespots) is the symmetry of the handaxes made by a particular male.

In support of the sexual selection hypothesis, Mithen (2005) argued that the overwhelming majority of handaxes are symmetrical (and essentially over-engineered for functional purposes); that the accumulations of handaxes seen at some sites may be the result of display arenas (essentially, leks); and, that the primary function of handaxes was to advertise "good genes" (an indicator model in which the female receives indirect genetic benefits) and therefore, most handaxes show little or no evidence of use wear.

TESTING MODELS OF SEXUAL SELECTION

According to Kohn's and Mithen's model, for handaxe morphology to be governed by sexual selection, females must have been making mating decisions on the basis of aspects of handaxe morphology that served as indicators of male quality (Machin 2008; Nowell and Chang 2008). For this to be true, it must also be true that:

1. hominins are attracted to symmetry, and *hominin females make mating decisions on the basis of symmetry* in morphological traits;
2. the quality of handaxe manufacture by extinct hominins was *governed at least in part by heritable variation*;
3. this heritable variation, that is related to the morphology of handaxes manufactured by extinct hominins, also was *related to male fitness*; and,
4. extinct hominin females made *mating decisions* at least in part on the basis of handaxe morphology.

At least three of these sub-hypotheses (2–4) are not testable because to do so would require observations that cannot be made. A previous critique of the "Sexy Handaxe Theory" in the context of indicator models of sexual selection briefly acknowledges that this absence of evidence makes the theory untestable "in one sense" (Machin 2008). In the previous section, we reviewed the types of evidence that modern biologists require to be able to test theories of sexual selection in living animals, and which is not available for studies of extinct hominins. In the following sections, we review the available evidence, as it were, related to these hypotheses. We explore alternative hypotheses explaining handaxe shape that are testable, and more parsimonious, than explanations relying on sexual selection.

SEXUAL SELECTION AND HUMAN PREFERENCES FOR SYMMETRY

Sensory bias or *sensory drive* models of mate choice evolution (Endler and Basolo 1998; Ryan 1998) do suggest that female preferences may initially evolve due to natural selection in contexts other than mate choice. It is true that humans demonstrate a generalized affinity for symmetry. In fact, all primates for which the question has been investigated favor symmetrical patterns over asymmetrical ones (Corbalis and Beale 1976; Uttal 1996). The ability to perceive different types of symmetry (vertical, horizontal, oblique) develops in a specific order during human ontogeny (Borstein and Stiles-Davis 1984). Furthermore, symmetry has been identified as an important element of design in such temporally and geographically diverse groups as the Yanomamo of Brazil, the Navaho, the Maori, the Inca, the ancient Maya, and colonial settlers in Virginia, and is a key feature of Islamic art (see references in Washburn 1999 and papers in Washburn 2004). When people are asked to create "visually pleasing designs" the vast majority create symmetrical patterns (Locher et al. 1998) and "adults tend to detect, discriminate, identify and remember symmetry better than asymmetry" (Bornstein and Davis 1984:637 and references therein).

Some biologists and psychologists suggest that symmetry preferences across species are simply a by-product of symmetrical patterning of neuronal connections in the brain. Others suggest an adaptive explanation, since many important environmental elements are symmetrical (Enquist and Arak 1994:169). The need to generalize many views of a single object from different positions and orientations may have led to a selection for preferences for symmetry (cf. Wenderoth 1997; see also Biederman 1995 for a related discussion on invariant object recognition). This *perceptual bias hypothesis* (Rhodes et al. 1998) is supported by simulation studies in which researchers trained connectionist networks (also known as artificial neural networks) to perceive patterns.

Similarly, preferences for symmetry often are attributed to information redundancy in symmetrical stimuli, a factor of obvious relevance to animals such as primates that rely so heavily on visual information for understanding and navigating their environment. In the study of shape, "good" patterns are redundant patterns "because the whole is so highly predictable from any part, while poor patterns, being unpredictable, are not redundant" (Garner 1970:34). "Good" patterns tend to be maximally symmetrical (i.e., symmetrical about the horizontal, vertical, left diagonal, and right diagonal axes). While there is evidence to suggest that all primates, including humans, have a preference for symmetry, this affinity may have evolved in the context of the evolution of our visual system, and not mate choice (see also Cárdenas and Harris 2007; Enquist and Johnstone 1997). In this context, if it does play a role in mate choice, this would properly be considered exaptive rather than adaptive.

Symmetry preferences also have been implicated in indicator models of sexual selection. Research conducted by zoologists, evolutionary biologists, and psychologists (e.g., Gangistad 1997; Gangistad et al. 1994; Gangistad and Thornhill 2003, 2004; Johnstone 1994; Möller 1992; Thornhill and Møller 1997; Watson and Thornhill 1994) suggests that phenotypic asymmetries, known as fluctuating asymmetries (FA), result from "random, stress induced deviations from perfect symmetry that develop during the growth of bilaterally symmetrical traits" (Johnstone 1994:172). Symmetry in male secondary sex characters may therefore be a reliable indicator of general health and, by extension, genetic quality and potential reproductive success. The level of FA in some species also is heritable, "and/or negatively correlated with one or more fitness measures such as viability, fecundity and growth rate" (Johnstone 1994:172). The results of recent studies focusing on humans, however, are equivocal. Developmentally stable individuals are buffered against some diseases and illnesses, but not others, and there is "little association between facial symmetry and either past, present or future health" (Milne et al. 2003 and references therein; Rhodes et al. 2001:43; but see Thornhill and Gangistad 2006).

SYMMETRY AND HOMININ MATE SELECTION

Even if sexual selection and the evolution of biological signals can be considered by-products of pre-existing symmetry preferences, it is still debatable how important a role these preferences played in mate selection among extinct hominins. What Kohn and Mithen (1999) do not make clear is that studies highlighting the role of fluctuating asymmetries in mate choice involve animals and insects such as swallows (Möller 1992), zebra finches (Swaddle and Cuthill 1995), and earwigs (Radesäter and Halldórsdóttir 1993), but not primates, let alone humans (Kappeler and Van Schaik 2004: 6). Kohn and Mithen write (1999: 522), "the symmetry of handaxes may have 'play[ed] on the perceptual biases of receivers to attract attention, provoke excitement, and increase willingness to mate (Miller 1997:96)'." Here, they quote an evolutionary psychologist out of context, implying that Miller supports the relationship between symmetry in handaxes and sexual selection when, in fact, the examples Miller gives relate to the sexual ornaments of organisms as phylogenetically distant from archaic humans as birds, fish, and frogs. In contrast, Kappler and Van Schaik (2004: 9) argue that there is "little evidence of female choice in primates, either in terms of the exclusive selection of particular mates or the consequences of such persistent choices on male phenotypes."

Studies investigating the relationship between facial symmetry and perceived attractiveness in humans are similarly inconclusive (e.g., Cárdenas and Harris 2007). There is some evidence to suggest that vertically symmetrical faces are considered more attractive by adults (e.g., Hughes et al. 2002; Perrett et al. 1999; Thornhill and Gangistad 1993, 1999; see also Gangistad and Thronhill 1998; Grammer and Thornhill 1994) and even by infants (Langlois et al. 1987; Muir 1994). Facial symmetry also is correlated with emotional and psychological health (Shackelford and Larsen 1997). Conversely, there are researchers who dispute the correlation between attractiveness and facial symmetry (Shakelford and Larsen 1999; Zaidel et al. 2005). A number of studies demonstrate that perfectly symmetrical transformations of real, asymmetrical faces were considered less attractive than the original faces by test subjects (e.g., Kowner 1996; Langlois et al. 1991; Samuels et al. 1994; see also Zaidel and Cohen 2005) and one study (Zaidel et al. 2005) suggests that 'very beautiful' faces can be functionally asymmetrical. It has been argued that it is the degree of averageness, and not symmetry of features, that is perceived as attractive (Langlois and Roggman 1990; Rhodes et al. 1998). Interestingly, while both average faces and symmetrical faces are *perceived* as healthier by human subjects, only average faces are actually honest advertisers of good health (and therefore, possibly, "good genes") based on patients' health records (Rhodes et al. 2001).

One final point about sexual selection directly concerns the appropriateness of applying this theory to primates including humans. According to Miller (1997: 107):

> "… sexual selection in multimale, multifemale primate groups is intense because the social context of mating is so complex and dynamic. Both sexes compete, are choosy, have dominance relations, and form alliances. Sexual relationships develop over weeks and years, rather than minutes. Under these relentlessly social conditions, reproductive success came to depend on mental capacities for "chimpanzee politics" (de Waal, 1982, 1989), "Machiavellian intelligence" (Byrne & Whiten 1988), "special friendships" (Smuts 1985), and creative courtship (Miller, 1993), rather than simple physical ornaments and short-term courtship behaviors, as in most other animals."

If these observations are true—and there seems to be ample evidence to support them (see references in Miller 1997)—and if it is valid to use non-human primates as a proxy for the behavior of extinct hominins, then it seems reasonable to believe that early hominins had an equally complex social life. It would appear that it may have taken more than symmetrical faces or, for that matter, symmetrical handaxes to attract a mate.

Further support for this point of view comes from the work of Kniffen and Wilson (2004), who emphasized the importance of non-physical traits on perceptions of physical attractiveness in modern humans. These traits include "niceness," intelligence, sense of humor, compatibility, willingness to work hard, availability (the so called "closing time effect"), and how much a potential mate appears to be attracted to the subject (Kniffen and Wilson 2004:89). Kniffen and Wilson (2004) emphasize that most research on human mate selection and attractiveness asks volunteers (strangers) to look at photographs of individuals and rate their attractiveness, but, in the past, hominins living in small groups would have been well aware of the non-physical qualities of their conspecifics. Through three elegant studies, they demonstrate that "nonphysical factors have a potent effect on the perception of physical attractiveness which can persist for decades…" (Kniffen and Wilson 2004: 99). They also found that non-physical traits influenced women's perceptions of attractiveness even more than men's. One of their studies, for example, asked students participating in an archaeological field school to rate the attractiveness of other participants at the beginning of the field season. Students were asked to do this once again at the end of the season. Kniffen and Wilson (2004) discovered that a participant's attractiveness rating was significantly affected by personality traits demonstrated during the excavation.

In sum, while human affinities for symmetry exist, it is not known whether these preferences evolved in the context of sexual selection, or are simple by-products of selection for general visual acuity and object recognition. Furthermore, evidence for the importance of symmetry in mate selection among primates is scarce. Currently, there is little empirical data to support the hypothesis that non-human primate females have preferences for male ornaments, or that female mate choice plays a significant role in non-human primate mate selection. Studies of facial symmetry and attractiveness in humans are inconclusive, as some suggest that it is the "averageness" of facial features, irrespective of symmetry, that correlates with perceived "beauty." Most studies of symmetry and attractiveness (and by extension, potential mate selection) are conducted among strangers, and do not include measures of perception of non-physical traits, which some researchers argue are crucial to mate selection in modern humans. Finally, if mate selection in non-human primates is too complex to be reduced to the symmetry of a male's physical ornaments, then it seems reasonable to suggest that early hominin social organization and mate selection were similarly too complex to be encompassed by such a simple explanation.

HERITABILITY OF CULTURAL TRAITS

Kohn's and Mithen's (1999) hypothesis further assumes that the quality of handaxe manufacture among extinct hominins was governed, at least in part, by heritable variation (see also Olausson 1998). To be part of an indicator model of mate choice, as they propose, this variation must have been related to male fitness, and females must have made mating decisions at least in part on the basis of handaxe morphology. Testing these conditions of Kohn and Mithen's hypothesis would rely on observations that cannot be made on extinct hominins. However, it is reasonable to assume that if there was selection on handaxe variability that favored symmetry, there should be a clear trend over time toward highly symmetrical handaxe assemblages in the archaeological record. This is an especially important condition of the hypothesis, since Kohn and Mithen (1999) argue that males were making vast numbers of these artifacts to advertise their qualities as potential mates, and so that females could witness the process. It is necessary that females were present when the handaxes are made, to ensure that the resulting artifacts are honest advertisers of good genes, as a poor knapper could simply have stolen a handaxe from a more skilled knapper. Those who are able to produce symmetrical handaxes would presumably have had differential access to mates, and benefited from differential reproduction and survivorship of offspring.

The question of whether there was, in fact, a trend toward increased symmetry over time in bifaces is complicated, with very few studies providing any empirical data (e.g., Saragusti et al. 1998) and *none* tackling this specific issue on a global scale. Wynn (2002, 2004a) argues that hominins increasingly "attended" to shape over time, and that this most often meant "an attempt at balance or symmetry" (but see McNabb 2004[1]). But this may be true only if we examine the Lower Paleolithic at a very coarse resolution. There is no evidence to suggest a *gradual* development of bifacial symmetry over time, with the symmetry of bifaces remaining unchanged for more than a million years (Wynn 2004b: 37).

Furthermore, if any pattern or trend does exist, it is complicated by regional, temporal and site-level variability. McNabb et al. (2004: 674) argue that symmetry is not in fact a common feature of South African sites. Some very early sites yield highly symmetrical artifacts such as the obsidian handaxes from Kariandusi (Gowlett and Crompton 1994) and some basalt handaxes from Gesher Benet Ya'aqov (Goren-Inbar and Saragusti 1996), while later sites exist with crude handaxes such as those from Fordwich (White 1998). Tremendous variability may be found within sites. At Hoxne, in England, the Lower industry is more refined than the Upper industry (Singer et al. 1993), while the reverse is true at Swanscombe (Graham and Roe 1970). There also are instances of what Wynn (e.g., 2004b: 33) has termed "intentional violations of symmetry" or "broken symmetry." As examples, Wynn cites the "bent" cleavers from Ismilia in Tanzania and the S-twist handaxes (with twisted edges) at Swanscombe. If we take this evidence at face value and consider these artifacts as intentional violations of symmetry, how are we to interpret these observations in light of the sexual selection hypothesis?

In essence, our ability to investigate this question is hampered not only by a lack of empirical studies, but also by the poor level of chronological control possible for this period. Many Acheulian sites are relatively dated on the basis of how symmetrical and standardized the handaxes found at those sites are (Nowell 2000; Wynn 2004b:34), with more symmetrical assemblages thought to denote late sites and less symmetrical assemblages taken to indicate earlier sites. The impossibility of using these data to detect trends regarding symmetry should be obvious.

THE ARCHAEOLOGICAL EVIDENCE FOR SEXUAL SELECTION

These points lead us to consider more closely the archaeological evidence for Kohn's and Mithen's (1999) hypothesis. According to Mithen (2005), the sexual selection model is supported by three types of archaeological evidence. First, he claims that an overwhelming number of handaxes are highly symmetrical. Second, he argues that there are large accumulations of handaxes at archaeological sites because these sites were essentially hominin leks (or display arenas) where females came to witness males making handaxes. Third, he explains that these handaxes show little or no evidence of any use because once they had served the purpose of advertising the knapper's "good genes" they were of limited use and were discarded. We will address each of these statements in turn, but first we consider what evidence we have of who made handaxes in the Pleistocene.

A Question of Sex

Central to Kohn and Mithen's (1999) argument is the assumption that it is males alone who are responsible for making symmetrical handaxes in order to attract females. It is clear, however, that we "have no basis for knowing whether handaxes were made by males or females" (Shennan 2002: 198; see also Bolger 2006; Machin 2008). In fact, we do not know the sex of those who made tools of any kind in the Paleolithic. What we can infer from the archaeological and fossil records are which *species* are in association with stone tools and/or faunal remains bearing cutmarks and which *species* are physically capable of the fine motor skills needed to manufacture a variety of stone tools (e.g., Marzke 2005) but we cannot determine sex from the data we have.

The assumption that males predominantly, if not exclusively, made and used stone tools including handaxes is symptomatic of a larger issue of how we assign gender roles in the Pleistocene in terms of subsistence, technology, and the creation of art that may be based more on presentism than scientific fact (e.g., see discussions in Bolger 2006; Brumbach and Jarvenpa 2006; Conkey and Gero 1984; Falk 1997; Gero 1991; McKell 1993; Nelson 2004; Roosevelt 2002; Wadley 1998; Weedman 2006b; Wiber, 1998; Zihlman 1989). Based on ethnohistoric, ethnographic, and ethnoarchaeological data, it is clear that women "made and used stone tools for shaving hair, tattooing, woodworking, fighting sticks, digging sticks, cutting tools, spear points, incising/decorating, and scraping hides" among other activities (Weedman 2006b: 270 and references therein; see also Bird 1993; Frink and Weedman 2005; Gero 1991; McKell 1993; Torrence 2001; Weedman 2005, 2006a).

Furthermore, in a detailed ethnoarchaeological study of hide scraping across a number of small scale, traditional societies, Weedman (2005, 2006 a, b) found no difference by gender in the use of space, in manufacturing process, in resulting tool morphology, or in raw material. In other words, the tools produced by men and women were archaeologically identical. Similarly, among tropical foragers, Roosevelt (2002: 365) notes, "the handaxe's descendants, the hafted stone axe or the steel-head hatchet or machete, are owned and used by women as well as men as everyday tools for cutting wood, digging and dispatching animals." Finally, it is worth noting that in non-human primate societies females make and use tools more often than males and for a wide variety of purposes (Roosevelt 2002 and references therein).

Symmetry in Handaxes

Mithen's perception that the majority of handaxes are highly symmetrical results from what Whitaker and McCall (2001: 571) have termed an "exaggeration and stereotyping of the archaeological record." By focusing exclusively on classic, teardrop-shaped artifacts, Mithen is artificially isolating types from what appears to be continuous variation in handaxe morphology (Bordes 1961; Débenath and Dibble 1994: figure 11.3).

There is, in fact, tremendous variation in the patterning of handaxes at continental, regional, and individual site levels. How can we explain, by Mithen's scenario, the so-called "Movius Line" (Movius 1948) which separates the handaxe-rich west from the handaxe-less east, or the total absence of handaxes from Europe east of the Rhine until Oxygen Isotope Stage 8 (White 2000), or the fact that the earliest occupation of Europe was characterized by non-handaxe assemblages? How were hominins in these areas advertising their "good genes" and attracting mates? At a regional level, examples include Roe's (1968) classic study of British handaxes that identified seven recurring groupings of handaxe shape, as well as variable expression of traits such as tranchet removals and twisted edges, and other unique features such as the Whitlingham "burins," within that small area alone (Nowell and White 2006). Finally, it is at the level of individual sites that variation, perhaps counter intuitively, is the greatest. While most sites do seem to show a modal tendency, variation is actually continuous, with the richer sites yielding examples of practically every conceivable permutation in handaxe form. One need only look at one of Roe's (1968) tripartite diagrams for British handaxes to appreciate the level of variation that is present in Acheulian assemblages (Nowell and White 2006).

The degree to which variability in handaxe shape is a result of factors such as blank morphology, raw material availability, technology of blank production, blank selection, retouch/resharpening (McPherron 2000; Nowell et al. 2003; see also Davidson and Noble 1993), size (Crompton and Gowlett 1993; Gowlett and Crompton 1994), function (e.g., White 1995 and see below; see also Dibble and McPherron 2006: 777), the imposition of a classification system that identifies pointed bifaces as "handaxes" and more rounded bifaces as "cores" (Nowell et al. 2003), and/or social practices and learning in isolated groups (Nowell and White 2006), is still a matter of much debate in Paleolithic archaeology. In fact, as White (2004: 671) argues, it is precisely the "lack of strong standardization in shape, symmetry, and manufacture" that has prompted researchers to study the effects of these types of factors on handaxe morphology. Mithen (2005: 188) dismisses the effects of blank and raw material size and shape by postulating that these factors affect handaxe morphology in "extreme cases" only, but these are certainly factors that warrant more exploration (see McNabb et al. 2004: 667).

Kohn and Mithen (1999) further argue that: (1) handaxes are much more symmetrical than they need to be for functional purposes; (2) many handaxes were retouched around the entire perimeter, making them difficult to hold and use as functioning tools; and, (3) handaxes "do not appear to provide sufficient degrees of improvement over plain flakes or choppers to justify that extra investment" (1999: 520) of time and labor. Whittaker and McCall (2001) counter that "even without a wrapping of hide or plant material a biface is no more likely to cut one's hand than a flake" (Jones 1981, 1994: 294). Similarly, White (1995) argues that there is evidence to support a preference for circumferential *working edges* (see also Jones 1994; McNabb et al. 2004: 667; Toth 1987). Whittaker and McCall (2001) further suggest that "while flakes are easier to make and can perform many of the same functions as handaxes, handaxes are in fact more efficient for some aspects of butchery and other work because they have more durable edges, are easier to hold and sometimes easier to use with precision and can be resharpened repeatedly" (see Jones 1981; Mitchell 1995).

Researchers from a variety of disciplines argue that symmetrical tools function more efficiently than asymmetrical ones (Bridgeman 2002; Coventry and Clibbens 2002; Deregowski 2002; Simao 2002; Wagman 2002). According to these authors, all things being equal, a symmetrical tool is easier to control, more comfortable to use because "more regular surfaces distribute the reaction force more evenly through the hand of the tool's user" (Simao 2002: 419), more ergonomic, and less likely to twist during use. Specifically, "symmetry puts the center of mass in the line corresponding to the direction of the motion of the tool at the instant of impact – thus avoiding torque and maximizing power" (Simao 2002:419). For these reasons, symmetrical handaxes are "safer, more predictable and more effective" (Bridgeman 2002: 403). These advantages mean that "more symmetric tools would have been more likely to be recreated and used by human ancestors, something that over eons led to the recorded tradition of ever more symmetric tools" (Simao 2002: 419). In other words, if it were true that handaxes did become more symmetrical over time, it could be the result of a positive feedback system based on utility (see Coventry and Glibbens 2002 for a discussion of evolving biomechanical algorithms that may underlie changes in knapping technologies).

It is clear that handaxes are more variable at continental, regional, and individual site levels than the sexual selection hypothesis assumes. The sexual selection hypothesis also does not address the absence of handaxes in some regions at different time throughout the Acheulian. Perfectly symmetrical handaxes actually represent a small percentage of handaxes, and these symmetrical types are not discrete from other, less symmetrical handaxe types. The degree to which handaxe morphology is the result of factors related to raw material, technology, typology, size, function, social practices, and learning is still a matter of much debate and should not be dismissed. More specifically what symmetry does exist may be explained by function, efficiency, precision, and safety.

Handaxe Accumulation

For Kohn and Mithen (1999: 522), "one of the most puzzling features of handaxes in the archaeological record is their great abundance at Acheulian sites." This characterization of Acheulian sites—envisioned as containing hundreds of handaxes that were discarded soon after their manufacture—is both exaggerated and stereotyped. While it is true that handaxes occur *en masse* at sites such as Melka Kunture (Ethiopia), Olorgesailie (Kenya), Isimila (Tanzania), and Kalambo Falls (Zambia), these sites are unusual, and far fewer handaxes are recovered from the vast majority of sites (Klein 2006).

The accumulation of handaxes at some sites is more likely the result of a gradual build up though loss, provisioning of place, or any number of taphonomic processes that took place over several hundred or more years (White, pers. com.). At issue are the effects of taphonomy and the resolution at which we may make observations at Paleolithic sites. Even the most high-resolution signatures, such as those from the stable paleo-landsurfaces at Boxgrove, probably represent accumulations of artifacts over several generations (Nowell and White 2006, n.d.). The accumulations of handaxes that are found at some Paleolithic sites are not, and cannot be interpreted as, snapshots in time as required by Kohn's and Mithen's hypothesis.

Use-Wear

Kohn and Mithen (1999: 522) are "puzzled" not only by the number of handaxes at some sites, such as Boxgrove, but also by the fact that many of them appear to be in "pristine condition." Currently, very few sites have been subjected to a systematic investigation of use-wear on handaxes, and "in many the depositional circumstances have left tools unsuitable for use-wear studies" (Whittaker and McCall 2001: 569). This is certainly the case at Boxgrove, where Mitchell (1997) argues that 57% of handaxes at Boxgrove were used for butchery, while the others show no trace of wear. While Mithen and Kohn apparently interpret this to mean the handaxes were never used, Mitchell (1997) is very clear that small amounts of movement in very fine silts have eradicated use-wear signs. Available data from use-wear studies suggest that handaxes were multi-purpose tools that were used for a variety of tasks including butchering and plant processing (Keeley 1980). Furthermore, the recurring association of handaxes with faunal remains (some with cutmarks on them) (Whittaker and McCall 2001) and data from modern experimental work (e.g., Mitchell 1995; Schick and Toth 1993) support the interpretation of handaxes as useful, multifunctional tools. Kohn and Mithen(1999: 520) themselves admit:

> "handaxes were general purpose artifacts; their functions are likely to have included the butchery of animals, cutting wood, slicing meat and chopping vegetables. Direct evidence, however, is quite scarce. *There are few cases where microwear studies have been undertaken*, such as on artefacts from Koobi Fora in Africa (Keeley and Toth 1981) and at Hoxne, England (Keeley 1980). Both samples showed a range of wear traces, indicating they had been used for a variety of tasks. Experimental work appears to confirm this, as handaxes are clearly effective for a range of activities..." (our emphasis).

The lack of systematic use-wear studies, the effects of taphonomic processes on our ability to conduct these studies, and evidence from the use-wear studies that do exist all challenge Mithen's (2005) contention that vast quantities of handaxes were produced only to attract members of the opposite sex, and then discarded.

CONCLUSION

Kohn and Mithen (1999) have contributed a novel explanation for Paleolithic handaxe morphology that is both intriguing and emotionally appealing, that draws from classical Darwinian theory, and that gives the impression of being testable, at least in part, given the available archaeological evidence. It is not surprising that a scenario of sexual selection and mate choice among extinct humans should capture the imagination of the general public and popular press. However, the general acceptance of this scenario in the archaeological literature and overall lack of critical evaluation of its principal assumptions is less easy to understand. In this review, we have outlined the primary assumptions and conditions underlying Kohn's and Mithen's hypothesis, evaluated the evidence for each, and suggested alternative explanations that are more parsimonious given the available data.

While there is evidence for symmetry preferences in modern humans, there is little evidence that these preferences are the result of sexual selection, and, in fact, most available evidence undermines the putative role of sexual selection in non-human and human primate evolution. In addition, some key conditions for Kohn's and Mithen's hypothesis cannot be tested because to do so would require impossible observations of extinct organisms. We cannot determine whether the quality of handaxe manufacture by extinct hominin males was governed at least in part by heritable variation because we cannot directly observe the makers, and we cannot identify their specific tools. We cannot determine whether this necessary heritable variation, if it existed, was related to male fitness, because we cannot make observations about the mating and reproductive success of extinct hominin males. We cannot know if extinct hominin females made mating decisions at least in part on the basis of handaxe morphology, because we cannot observe the behavior of extinct hominins. Hypotheses about the role of sexual selection in the evolution of extant animals are not simple to test, as any survey of the relevant literature will make clear, and testing such hypotheses requires the ability to collect basic observational and experimental data about heritable variation, mate choice, and reproductive success from the specific organisms of interest. In the absence of such data, hypotheses about sexual selection necessarily remain in the realm of speculation.

Kohn's and Mithen's sexual selection hypothesis for handaxe morphology also is unsupported by the available archaeological evidence. This hypothesis relies on a stereotyped characterization of variation in Acheulian handaxe shape, both within and between sites, and ignores what is known about the effects of technological limitations, typological practice, and factors that may be related to culture or style on handaxe morphology. Handaxe morphology, and explanations for its variability, remain issues of considerable debate in the archaeological literature. The best available evidence strongly suggests that variation in handaxe morphology is governed by a number of complex factors that differ in influence over time and space, rather than a single overarching mechanism such as sexual selection. As with most questions of interest in Paleolithic archaeology, we are better served by context-specific, historically situated explanations rather than monocausal scenarios, particularly when our desire is to understand the form and function of an artifact such as the handaxe, which is found in the record, in one form or another, for more than 1.5 million years.

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