Life Histories, Metapopulation Ecology, and Innovation in the Acheulian

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ABSTRACT

In the course of the evolution of the genus *Homo,* the most profound developments in life history parameters seem to have occurred in the Lower Pleistocene. Yet Acheulian industries are widely seen as having remained essentially unchanged for some 1.3 million years or more. In reality, however, although the Acheulian did not develop in a cumulative or directional manner over its long history, it nevertheless displayed considerable levels of typological and technological diversity and variability at continental, regional, and local levels. It is at the local level that this variability is at its greatest, with prepared core technologies regarded as characteristic of the succeeding Middle Paleolithic and Middle Stone Age appearing sporadically and ephemerally in the Acheulian. It is our contention that this pattern of local, short term variability combined with global long term stasis cannot be accounted for by models asserting that the hominin makers of the Acheulian lacked the cognitive capabilities of their evolutionary successors. Instead, we argue that Acheulian hominins were cognitively capable of innovative technical behavior and often displayed it; but that, despite structural life history parameters that approached those of living *Homo sapiens*, relatively short childhood, juvenile, and adolescence phases, combined with small local group size, constrained the social and developmental scope for innovation. Furthermore, we argue that metapopulation-level social, demographic, and ecological dynamics in the Acheulian, relating to group size, foraging ranges, and levels of individual migration, served to limit the lifespan of local groups and thereby reduced the likelihood of innovative behaviors disseminating through social networks and becoming fixed in cultural repertoires before the originator population became extinct. We explore the idea that the transition from the Acheulian to the ensuing Middle Paleolithic and Middle Stone Age was therefore driven not by evolutionary developments in hominin cognitive capacities, but by changes in life history and metapopulation factors.

INTRODUCTION

In the course of the evolution of the genus *Homo*, the most profound developments in life history parameters seem to have occurred in the Lower Pleistocene (papers in Thompson et al. 2003). Yet the Acheulian industries that dominate the archaeological record of Africa and large parts of Eurasia from around 1.6 million years ago appear to have remained largely unchanged typologically and technologically for some 1.3 million years or more, maintaining through that timespan and geographic range the essential signature of large cutting tools (LCTs)/handaxes combined in varying proportions with a simple core-and-flake component. So striking is this apparent technological stasis that the Acheulian has often been described as 'monotonous,' 'stagnant,' and as a 'long oscillation' (Isaac 1972, 1976) with no directional trend (Leakey 1975). Yet, on closer examination, the archaeology of the Acheulian furnishes evidence for widespread and relatively frequent technological innovation, especially in terms of the development of diverse prepared core reduction technologies (PCTs) such as, but by no means limited to, the Levallois technique. Herein lies the apparent contradiction of the Acheulian—despite considerable variability and even novelty in lithic technological behavior, there is little or no evidence for *cumulative* net directional change in lithic technology in the long term.

We contend that this pattern cannot be accounted for by models asserting that the hominin makers of the Acheulian lacked the cognitive capabilities of their evolutionary successors (*contra* Binford 1989; Isaac 1972; Klein 1999; Mithen 1996). Instead, we argue that an exploration of the factors that impinged upon the adoption and transmission of novel behaviors in Acheulian society at and between the local and regional scales, and in and between the short and long terms, is required if this problem is to be illuminated. In this paper we discuss the significance of Lower Pleistocene developments in hominin life history strategies and parameters, and of a hominin metapopulation ecology, for our understanding of this problem. Our conclusions are

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preliminary, but aim to address one of the more intriguing elements of the 'muddle in the Middle.'

ACHEULIAN HOMININ LIFE HISTORIES

Life history can be understood as 'the allocation of an organism's energy for growth, maintenance and reproduction…[and is] a life strategy adopted by an organism to maximize fitness in a world of limited energy' (Dean and Smith 2009: 115), as reproductive turnover or as 'the speed of life' (Stearns 1992). Following this metaphor, it is often said that, amongst mammals, primates have the slowest life histories (Harvey and Clutton-Brock 1985; Robson and Wood 2008; Zimmermann and Radespiel 2007) and, by extension, that humans experience the slowest life histories of all the primates. However, the emerging picture of human life history is at once more complex and more elegant (Nowell 2010 in press).

As paleoanthropologists, we are accustomed to thinking in terms of organisms pursuing either 'k' or 'r'- reproductive strategies. Relative to r-strategists, k-strategists reach the age of reproduction more slowly and have fewer offspring, but invest more in each. While k-strategists thereby enhance the quality of their offspring, the drawback to a slow reproduction strategy is an elevated risk of death before reproduction (Dean and Smith 2009: 101; Robson and Wood 2008). Humans, however, are unique in that they display elements of an r-strategy within the larger life history of a k-strategist. Specifically, they have a long gestation period, a large brain, mature more slowly with females reaching the age of reproduction later, experience an extended dependency period, and enjoy increased longevity; but they have also evolved shorter birth spacing, earlier weaning, and have more dependents than expected for an ape that matures at the age modern humans do (Robson and Wood 2008). Modern humans display a reproductive pattern that works twice as fast as that of the great apes (Dean and Smith 2009: 115)—something that Wood (1994) has described as secondary r-selection. Added to this unique combination of features is a suite of derived elements—concealed ovulation, helpless young, rapid postnatal brain growth in infants, continued post-weaning dependency, paternal care, and vigorous post-menopausal life in females (Bogin 1997; Dean and Smith 2009: 115; Hawkes et al. 2003; Kaplan 2002; Leigh 2004, 2012; Robson and Wood 2008; Zimmermann and Radespiel 2007). Thus, modern humans have developed a strategy of producing high quality offspring while at the same time reducing the risk of early mortality by 'living fast' in some respects, within an overall pattern of 'living slow.'

These life history properties impact on hominin ranging behavior, locomotion, diet, energetic requirements, subsistence strategies, childbirth, ontogenetic development, demography, communication, and technology (Nowell 2010), and significant changes in these variables coincide with the emergence of Lower-Middle Pleistocene hominins whose life histories represent a significant divergence from those of apes (Krovitz et al. 2003; Nowell 2010; Tardieu 1998). For example, it is generally agreed that fully obligate terrestrial bipedal locomotion, increased population size, extension of geographic range (Antón et al. 2002; McKee 2003), the appearance of body proportions and levels of sexual dimorphism within the modern human range, and a shift towards meat consumption (Aiello and Wells 2002; Shipman and Walker 1989) all developed first in *Homo erectus sensu lato*. This dietary shift resulted in a reduction in gut size and a 20–60% increase in brain size relative to earliest *Homo* (Aiello and Wells 2002; Aiello and Wheeler 1995). Such significant increases in brain and body size, together with a widening of the shoulders, may have led to the birth of more helpless (secondarily altricial) infants, and also to 'obligate midwifery' (Jolly 1972, 1999, 2003; Rosenberg 1992; Trevanthan 1987; Trevanthan and Rosenberg 2000; see also Walrath 2003 and comments therein; but see Krovitz et al. 2003 for concomitant social implications).

Recognizing that 'brain size and body size have significant correlations with a variety of maturational processes such as age at sexual maturity, maternal age at first birth and gestation length,' Kennedy (2003) has argued that Lower/Middle Pleistocene hominins reached sexual maturity around age 13 with a female's first birth occurring somewhere between 15 and 16.5 years of age; these estimates fall within the modern human ranges for those life history variables. Hemmer (2007: Table 19.14) presents similar inferences.

Some researchers have argued that it is with *Homo erectus sensu lato* that we first witness the extension of female life expectancy significantly beyond menopause (Aiello and Key 2002; Bogin and Smith 1996; see also Robson and Wood 2008). This is the so called 'grandmothering hypothesis' which proposes that grandmothers and great aunts were involved in the provisioning of children, thereby permitting earlier weaning and a consequent reduction in interbirth spacing (Hawkes 2003; Hawkes et al. 1997, 1998, 2003; O'Connell et al. 1999; but see Monge and Mann 2007). This hypothesis is controversial; recent studies have pointed to the absence of supporting fossil evidence and have instead suggested an increased level of paternal investment in offspring care by *Homo erectus sensu lato* males relative to earlier hominins (Krovitz et al. 2003).

The size of local groups or populations has been estimated at just over one hundred individuals, which might represent an increase over that in earlier *Homo* of 20–25% (Aiello and Dunbar 1993). On the basis of studies of endocranial casts and the suite of behavioral changes described above, particularly niche expansion and handaxe manufacture, some paleoanthropologists have argued for increased complexity in vocal communication with *Homo erectus sensu lato* relative to non-human primates, suggesting that the species may have been capable of a proto-language or 'pre-syntactic' language (Bickerton 1992; Holloway 1996; Petraglia et al. 2005; Roberge 2012; Tallerman and Gibson 2012: 29; Tobias 1995; but see MacLarnon 2012; MacLarnon and Hewitt 1999, 2004 for a contrary view with respect to Lower Pleistocene *Homo erectus*). At the same time there is little evidence for the mediation of social life through material culture symbols (Chase and Dibble 1987; d'Errico and

Nowell 2000; d'Errico et al. 2003).

While certainly not modern in their lifeways, the life histories of Lower/Middle Pleistocene hominins represent a substantial departure from strategies practiced by apes, australopithecines, and earliest *Homo* and align them more closely with modern and Upper Pleistocene humans.

ACHEULIAN TECHNOLOGICAL SYSTEMS

The apparent stasis in Acheulian technological practices stands in stark contrast to this transformation in life histories. While many older classificatory schemes attempted to document (or imagined; see O'Connor 2007) gradual cultural trends towards increasing sophistication in handaxe shape and sophistication through time (Breuil and Koslowski 1931, 1932, 1934; Commont 1908; Gilead 1970), most modern workers are skeptical of such evolutionary schema, see little directional change, and take greater account of a range of factors influencing handaxe form. Improvements in the dating of Acheulian assemblages have demonstrated that one cannot equate 'cruder' with 'older' and that particular forms did not appear and disappear in a progressive sequence. Local and regional variations in handaxe form are often attributed to mechanical factors such as raw material shape, type, and availability (e.g., Jones 1979, 1981; White 1998), resharpening (Jones 1994; McPherron 1994), or function (Roe 1981). In sum, the archaeology of the Acheulian seems to document a technological conservatism of unparalleled magnitude, a conservatism usually attributed to the limited cognitive and linguistic capabilities of the hominins involved (Binford 1989; Isaac 1972; Klein 1999; Mithen 1996).

This portrait of the Acheulian and its makers does not withstand scrutiny. It is incontrovertible that there is a very long-term stasis in the overarching Acheulian technological repertoire, and that it is impossible to order variability in terms of sustained directional trends. We must also acknowledge that poor chronological control and low-resolution secondary-context signatures at many sites, together with the patchy, palimpsest nature of the Acheulian archaeological record, frequently conspire against attempts to reveal both cumulative developments and major ruptures in technological behaviors. Even the most high-resolution signatures, such as those from the stable paleo-landsurfaces at Boxgrove, Sussex, probably integrate discard behavior over a timespan of several generations (Pope and Roberts 2005; Roberts and Parfitt 1999). Yet it remains true that Acheulian technological and typological variability can be observed and demonstrated. Although the available resolution precludes fine-grained dating of this variability, that does not mean we must dismiss it as mere noise. If one accepts that the very simplicity of Acheulian technology itself constrains the scope for innovative modification, and if diversity on small spatiotemporal scales is embraced rather than suppressed in the synthesizing search for manageable order, then it becomes apparent that the Acheulian was actually more dynamic than is generally perceived.

On the other hand, if Gowlett (2005) is right to argue that Acheulian handaxes were made in many forms from a wide variety of materials as the result of the 'artisan's choice,' then why do we not see much more diversity in Lower Paleolithic technologies? The key to this conundrum lies in the adoption of a multi-scale perspective. The Acheulian was largely static over very long periods of time at continental scales, but there are robust long-term patterns of difference *between* continents, while Acheulian technical behavior was much more dynamic at short-term local scales (Nowell and White 2010).

Systematic variability between continents in handaxe form has been demonstrated by Wynn and Tierson (1990), who revealed subtle but significant differences in this respect between Europe, India, Africa, and the Near East in the Later Acheulian. The differential occurrence of cleavers—very common in Africa and India, but largely missing from northwestern Europe—is another example of high-level patterned variability within the Acheulian (White 2006). Such variability was recognized in Petraglia and Korisettar's (1998) edited volume, subtitled *The Rise and Diversity of the Lower Paleolithic Record*. Existing over and above these very large-scale realms of geographical variability within the Acheulian are well-established distribution patterns of Acheulian and non-Acheulian technologies in the Lower Paleolithic, such as the absence or rarity of handaxes in East Asia (Movius 1948; Schick 1994; but see Petraglia and Shipton 2008) and in Europe east of the Rhine before MIS 8 (Bosinski 1995; Hopkinson 2007a; McBurney 1950; Svoboda 1989; White 2000).

Variability in handaxe form is also evident at the regional level. Roe's classic study of British handaxes (Roe 1968) identified seven groupings of handaxe shape, as well as variable expressions of traits such as tranchet removals and twisted edges, together with other unique features, such as the Whitlingham 'burins,' within that small area alone. Studies of terrace sequences throughout Europe have revealed similar patterns that were in fact recognized at the very inception of Paleolithic studies (e.g., Evans 1860, 1862). One must also not forget the enigmatic and still unsatisfactorily explained fluctuations between Acheulian and non-Acheulian signatures within regions (e.g., Mussi 1995 for Italy; White 2000 for Britain). It is clear that core-and-flake technology in the British Clactonian is effectively identical to that of the Acheulian (McNabb 1992; White 2000), but there remains disagreement as to whether the Clactonian is merely an artifact of archaeological taxonomics and of sampling effects (e.g., Ashton et al. 1994), whether bifaces form part of its technical repertoire (McNabb and Ashton 1992), and whether it is a pan-British phenomenon (White 2000; White and Schreve 2000) or is restricted to the Thames Valley (McNabb 2007).

It is, however, at the local, assemblage, and short-term scales that handaxe formal variability is greatest. While most Acheulian assemblages by site and horizon seem to show a modal central tendency in handaxe morphology, variability about this central tendency is often substantial, with the richer sites yielding assemblages containing practically every conceivable permutation in handaxe form. Even the Boxgrove assemblage, famous for its well-made, standardized ovate handaxes, shows higher levels of formal variation than is usually recognized (Pope, personal communication 2007).

Acheulian variability is not restricted to the morphologies of handaxes and other bifacial LCTs. The core-and-flake component of Acheulian toolkits is dominated everywhere by simple migrating plane core methods, but there is nevertheless a considerable record of the localized and sporadic occurrence of prepared core technologies typically associated with the Middle Paleolithic and Middle Stone Age. By innovatively combining the Acheulian technical elements of bifacially-configured cores (handaxes) and the production of flakes by *débitage* techniques into a unified strategy for flake production, Acheulian knappers could, and often did, develop prepared core reduction technologies (White and Ashton 2003).

As with handaxes, PCTs in the Acheulian display variability on local, regional, and continental scales. They occur significantly more frequently in Africa and the Levant (Beaumont and Vogel 2006; Goren-Inbar 1992: 75) than in Europe. Within Africa numerous PCT variants exhibit particular regional and temporal distributions. Victoria West (VW) technology can be dated to between >1.1 mya and 780 kya at South Africa sites such as Canteen Koppie, Kathu Pan, and Wonderwerk (Beaumont and Vogel 2006; Herries 2011: 7; McNabb 2001). In the Casablanca region, however, VW technology is much younger (commencing around 430 kya at Sidi Abderrahman) and follows a different developmental sequence (Raynal et al. 2001, 2002; Rolland 1995; White et al. 2011: 59–60). Comparable patterns of regionally-specific PCT variants are known elsewhere in the African Acheulian, such as the Tachengit-Tabelbala cores of the Maghreb, and the 'Bent Levallois' and Safaha core reduction techniques of Ethiopia and the Nile Valley, respectively (White et al. 2011, and references therein). In addition to these regional core reduction phenomena in the African Acheulian, there are also localized examples such as the giant prepared cores known from Rift Valley localities including the Middle Awash, Koobi Fora, the Kapthurin Formation, Olorgesailie, and Olduvai (Madsen and Goren-Inbar 2004; Tryon 2006), and the true prismatic blades and cores dated to 500 kya from the Kapthurin Formation (Johnson and McBrearty 2010). Critically, these outbreaks of apparently precocious reduction techniques do not represent clear cultural transitions or constitute persistent and culturally continuous traditions in the African Acheulian, even at the local level. Instead, the archaeological patterning strongly suggests repeated, innovative but short-lived elaborations of already-existing technological procedures.

PCTs perhaps occur most systematically in Acheulian contexts in the Levant (Goren-Inbar 1992, 75). At Gesher Benot Ya'aqov, Israel, archaeological horizons deposited between 760 and 660 kya (Sharon et al. 2011: 388) have produced Levallois, Kombewa, and giant cores, the latter including both hierarchical and 'sliced' variants (Goren-Inbar et al. 2000; Sharon 2009). It is interesting to note that, although the *chaîne opératoire* through which LCTs were produced from large flake blanks remains virtually unchanged throughout the depositional sequence at the site (Sharon et al. 2011), the primary reduction technology for the production of those large flake blanks is much more variable.

Beyond Africa and the Levant, PCTs in the Acheulian are less common. Hierarchically-organized giant cores, used for the production of LCT blanks, are known from Isampur Quarry, India, where they probably date to 1.2 mya (Petraglia et al. 1999), while Levallois reduction is reported from a number of Acheulian sites in Europe, including Cagny-la-Garenne, northern France, and Swanscombe, southern England (Tuffreau 1995). There is also at least one claimed European instance of the Victoria West technique, at Petit-Spiennes, Belgium (Watteyne 1985).

Of course, persistent formal variability between continental-scale Acheulian provinces remains compatible with a conception of Acheulian hominins as fundamentally conservative (e.g., Petraglia et al. 2005) and unable to innovate practices beyond those specified by long-lived cultural repertoires and their range of possible adaptive responses to external forcing factors. However, the synchronic variability within regions, and even more especially the technical variability within the Acheulian at assemblage, local, and short-term scales, is much more difficult to reconcile with such a view. The range of forms and techniques visible at these spatiotemporal scales suggests that Acheulian hominins had room for maneuver, and the cognitive capacity, to effect knowledgeable modifications of tools and techniques in ways that were not wholly specified by technical tradition or by determined responses to external factors. So, while it remains true that there is little or no demonstrable long-term cumulative change in Acheulian lithic technological behavior within continental scale industrial provinces, it is equally clear that the Acheulian was not the same everywhere or every-when. The paradox of the Acheulian is that significant variability at local and short-term scales did not lead, by natural selection or any other mechanism, to net, directional developments in technical practices in the long term.

LIFE, THE HANDAXE, AND THE HOMININ

The above discussion leaves us with an intriguing picture of a fractured biological and behavioral system. While the fundamentally modern life history pattern is already in place with *Homo erectus/ergaster* in the Lower Pleistocene and certainly appears in Europe early in the Middle Pleistocene with the emergence of late *Homo erectus sensu lato* or *Homo heidelbergensis*, the industries of the Acheulian are anything but modern in their patterning. How can we explain this conundrum?

Here we offer some tentative thoughts. In an earlier paper two of us (Nowell and White 2010) drew a semantic distinction between two related yet subtly different elements of change—inventiveness and innovation. We defined *inventiveness* as the ability to be creative within the prevailing repertoire of technical skills, whereas we used *innovation* more specifically to describe the emergence of totally novel traits[1].

It can be argued, from an adaptive perspective, that the initial surge of technological developments in the early Acheulian—the systematic production of large bifacial cutting tools—was enough to support post-Oldowan life history until the next major rupture. Changes in Lower Pleistocene life histories—the introduction of a childhood phase, greater levels of care-giving by old and skilled individuals, changes in mobility and terrestriality—facilitated the Acheulian and were components of a successful adaptive strategy, but there was no directional selection exerted on stone tool technologies. From this standpoint, Acheulian technology was entirely fit for purpose and flexible enough to be adapted to the heterogeneous needs, strategies, or preferences of a mobile lifestyle, responses to situation, and idiosyncrasy. Furthermore, given the simplicity of Acheulian technology, the scope for innovative development was limited.

Yet this argument, though seductively simple, cannot be sufficient. Traits, whether anatomical, physiological, or behavioral, whether biologically or culturally transmitted, are never 'wholly fit for purpose' in themselves. A trait's fitness in an evolutionary sense is always, in part, a function of other traits present in the population. Given the typological and technological variability present in the Acheulian, how can the failure of more adaptive or optimal forms to proliferate through time at the expense of those that were less so be explained by reference to simple selective and adaptive processes? Even more telling is the sporadic occurrence in the Acheulian of PCTs typical of the Middle Paleolithic and the Middle Stone Age. If PCTs were adaptively advantageous relative to the fundamental Acheulian technologies of bifacial core tools and simple migrating plane *débitage*, then why do they not proliferate as technological behaviors for hundreds of millennia after they first appear in the Acheulian? If they were not, why would they eventually become widespread, even dominant, technological practices in both Africa and western Eurasia? A naïve functionalist approach to adaptation and cultural change cannot answer these questions.

Instead one must first understand technological behaviors as skilled and knowledgeable practices transmitted in time and space through networks of social relationships. Second, it is essential that Acheulian technical practices are conceptualized not as an independent realm of behavior, but instead as embedded in other social and behavioral traits, practices, and structures. The social environments in which technological behaviors are embedded can promote conformity and militate against innovation, in both contemporary societies (e.g., Baerveldt and Snijders 1994; Efferson et al. 2008) and in captive chimpanzees (Hopper et al. 2006; Whiten et al. 2005). Equally, they can display low social conductivity so that such innovations as do arise locally are unlikely to disseminate and persist. To overcome the Acheulian paradox of variability and stasis we need to go beyond function and adaptation to explore the social conditions under which new technological practices, whether adaptively advantageous or not, are generated and disseminated.

ACHEULIAN INDUSTRIES, METAPOPULATION ECOLOGY, AND THE PERSISTENCE OF INNOVATIONS

Shennan (2001) has argued elegantly, on the basis of mathematical modeling, that as hominin population size increases so do the rate of cultural innovation and the likelihood that advantageous cultural traits will be maintained and that harmful ones will be selected against. Hopkinson (2011) and Powell et al. (2009), however, have argued that, rather than increase in gross population size, the key factor is the dynamic relationship between the local population level at which innovation originates, and the regional population level to which a locally-arisen innovation must spread if it is to persist. Such an approach to understanding the patterning of persistence and novelty in the Acheulian requires a consideration of Pleistocene hominin metapopulation ecology (Hopkinson 2011).

Regional populations of any terrestrial species are comprised of local populations, just as local populations are comprised of individuals. This regional 'population of populations' is the *metapopulation*. Species will persist regionally at the metapopulation level despite the susceptibility of local populations to extinction provided that, on average, each local population produces at least one daughter population before it becomes extinct (Levins 1970). Within a metapopulation, regional gene flow and, in the case of hominins, *knowledge* flow (the social transmission of learned practices or behaviors) is facilitated or impeded by the rate and character of connections, encounters, and relations between local populations. Regional metapopulations can therefore be conceived as networks in which local populations are nodes between which individuals, genes, and knowledge flow in particular and variable ways.

An understanding of the social dynamics of innovation in the Acheulian must therefore embrace two different social scales—the local population or band, and the regional metapopulation. These correspond in turn to two dimensions in the social process of innovation—the generation and local adoption of novel behaviors, and their subsequent dissemination (or otherwise) through space and time. Developments in hominin life history parameters can be shown to condition the former, and are discussed below. The precepts of metapopulation ecology, on the other hand, can cast light on the latter—the likelihood that novel behaviors, once arisen in a local population, will disseminate or diffuse to other local populations in the metapopulation, and persist therein.

It is presumed here that, although innovation is necessarily a social process, it is at the level of the individual social agent, or of small cliques of intimate individuals within a local population, that novelty arises. Given the general hostility of small social groups to novelty (e.g., Baerveldt and Snijders 1994; Efferson et al. 2008; Hopper et al. 2006; Whiten et al. 2005) it is to be expected that most novel behaviors in the Acheulian were quickly suppressed and never attained a sufficient level of adoption to become archaeologically visible. Equally, on those occasions when a novel behavior was adopted within a local population (for whatever reason, such as the social status of the innovator or imitator), the very same small-group conservatism would serve to maintain it within that local population. At that point, the novel behavior becomes available to spread to neighboring populations through the networks of flows within the metapopulation. This process is embedded in the social, demographic and ecological dynamics of the metapopulation.

If metapopulations constitute networks of knowledge flows in which local populations are nodes, then because local populations are chronically prone to extinction over time, the likelihood of any locally-arisen innovation transmitting to another local population is broadly proportional to the life span of local populations. Increased band longevity (i.e., reduced local extinction rate) will therefore promote the transmission of innovations between bands, while a shorter local band lifespan will increase the likelihood that a local population will disappear, together with its innovations, before those innovations spread within the metapopulation (Hopkinson 2011; Premo and Kuhn, 2010). In a hominin metapopulation of short-lived local bands, one would expect to see sporadic, localized, and ephemeral episodes of innovative behavior. The factors governing local population longevity are therefore of critical importance in determining the susceptibility of the Acheulian to behavioral change in time and space. Metapopulation ecology recognizes three major factors that condition local population lifespan—local population size, territorial range, and individual migration.

LOCAL POPULATION SIZE

A local population of any discontinuously distributed terrestrial animal species will become extinct as a discrete entity when its size (i.e., the number of component individuals) becomes too small to maintain viability. The major cause of local extinction is stochastic variation through time in population size (Hanski 1999: 28). Consequently, the larger the local population, the longer it is likely to survive. (Foley 1994, 1997). Larger populations are also less vulnerable to disabling stochastic variations in parameters such as age structure and sex ratios, and are also more attractive to immigrants (Kuussaari et al. 1996). Smaller local populations, by contrast, have shorter lifespans and are unlikely to be able to augment their numbers through immigration. For Paleolithic hominins, this means that, the larger the local band, the greater the probability that any innovative practices that emerge and become fixed in it will transfer to another band before the innovator band itself becomes extinct. Large group size has also been shown to promote fissioning in terrestrial primates (Henzi et al. 1997), enhancing the likelihood of the formation of daughter bands that reproduce the behavioral practices of the parent band. It is therefore significant that, while hominin endocranial capacities in the late Lower and early Middle Pleistocene were significantly higher than that of preceding hominins, they are also significantly lower than those following the burst of encephalization that occurred around 300 ka (Aiello and Dunbar 1993). This has been interpreted in terms of the 'social brain hypothesis' (e.g., Dunbar 1992, 2009; Kudo and Dunbar 2011; Pawlowski et al. 1998; Reader and Laland 2002; Shultz and Dunbar 2007) to imply an increase in the number of inter-socializing individuals, and thus of local group size, coinciding with the shift from the Lower to the Middle Paleolithic and the Early to the Middle Stone Age (Aiello and Wheeler 1995; Ruff et al. 1997).

TERRITORIAL RANGE

Mosaic landscapes are complex ecological systems in which vegetation patches at different successional stages, of different sizes and shapes, and different species composition, coexist dynamically. In addition, different components of mosaic landscape ecosystems respond preferentially to particular wavelengths of climate cyclicity. Consequently mosaic landscape history is *asynchronous* in that the component spatial, species, and functional elements of mosaics exhibit different, often localized, responses and response rates in the face of climate change. This was particularly so in the Pleistocene, which was subject to high-amplitude Dansgaard-Oeschger climatic periodicities on wavelengths of a few millennia in addition to shorter-wavelength centennial and decadal, and longer-term Milankovich-scale, climatic cycles. This means that Pleistocene environmental change through time also had an important spatial component (Hopkinson 2007a, 2007b, 2011). The risk of extinction faced by local populations as a consequence of resource and habitat loss arising from climate change events is therefore conditioned by the size of territorial foraging ranges. The larger the range, the greater the likelihood that, although there might be a climatically-forced loss of key resources from one or more parts of the range, those resources, or functionally equivalent substitutes, will persist somewhere within its boundaries (Short and Turner 1994).

For Pleistocene hominins, an increase in territorial range would therefore reduce the risk of local band extinction through resource loss and thereby contribute to increased local band longevity. From this perspective it is highly significant that, in Europe at least, the transition from the Acheulian to the Middle Paleolithic saw a major increase in lithic raw material displacements (Féblot-Augustins 1997a, 1997b) and the first systematic incorporation of lowlands and uplands into mobility strategies (Hopkinson 2007a, 2007b).

IMMIGRATION, EMIGRATION, AND FISSIONING

This aspect of Pleistocene hominin metapopulation dynamics presents particular difficulties of archaeological visibility. However, modeling of the impact of migration rates on innovation retention and survival by Powell et al. (2009) supports the contention that between-group individual migration is an important factor conditioning innovation retention and loss at the metapopulation level. While Powell et al.'s mathematical simulation rests upon some unrealistic assumptions (e.g., that all local populations in the metapopulation are of equal size, and that migratory movements can be represented through random walk), it nevertheless shows that innovation retention within a metapopulation increases with both the frequency and distance of migratory individual migratory movements.

In ecological reality, of course, individual migratory movement is frequently not random or stochastic. Within a metapopulation some local populations are likely to be more attractive than others to immigrants, so it is probable that the net flow of migratory movement will be asymmetrical. Local populations or bands can therefore suffer extinction, even if their birth rate exceeds their mortality rate, if their net rate of individual emigration exceeds their growth rate; conversely, local groups can persist despite mortality exceeding natality providing they can attract sufficient immigrants. The factors that impinge upon rates and directions of migration are therefore of some importance to this question. It has already been noted that large local populations encourage immigration while small local populations do not; and that large local populations are more inclined to fissioning. A further significant determinant of migration rate and direction is its *cost*. The major cost of migration is the risk of death (Ims and Yoccoz 1997; Olivieri and Gouyon 1997). Structurally high migration costs will ensue where the habitat between local populations is dangerous, resource-poor, or unfamiliar to the migrant; if the would-be migrant is at risk of rejection by a local population they seek to join; and, if local populations are sparsely distributed in space so that the distances separating them are high. All of these conditions would have the effect of inhibiting emigration and depressing immigration.

The 'packing density' of local populations in space therefore has significant consequences. Where local populations are sparsely distributed, high migration costs limit the rate of migration and can lead to local population isolation. Isolated populations are less likely to experience mutual encounters or to exchange members, so low-density local population spatial distribution acts as a brake on the transmission and retention of innovations. This is compounded by the likelihood that isolated local populations are small, making it difficult for them to augment their numbers by attracting immigrants (Hanski 1999: 17). Thinly distributed local populations thus tend to be shorter lived than those that are more densely packed in space. Again, Powell et al.'s (2009) model also suggests a clear link between local population density and the rate of innovation retention in a hypothetical metapopulation.

Another factor that should be mentioned here is the so-called *source-sink* effect (Pulliam 1988). Where a region inhabited by a metapopulation consists of one or more high-value habitat areas, local populations in those areas are likely to be larger, more densely packed, to experience higher growth rates and extended longevity, and to produce daughter populations that migrate to surrounding low-value habitat areas. Population pressure in core habitats can therefore maintain metapopulation presence in marginal habitats where, because of resource constraints, local populations are liable to be smaller, more widely distributed and shorter-lived. This has the counter-intuitive consequence that behavioral innovations in marginal habitats, where they are more likely to offer survival advantage and thus to be selected for, are less likely to disseminate through the metapopulation than innovations arising in core areas where already-existing behaviors are under less selective pressure to change.

These considerations provide a powerful explanation for the observed pattern of the Acheulian archaeological record. Evidence from endocranial capacities, raw material transport, and time-space site distribution data suggests that Acheulian local population sizes, territorial ranges, packing densities, and, by implication, migration rates were limited relative to the ensuing Middle Paleolithic and Middle Stone Age. From a metapopulation ecology perspective, this would predict precisely the pattern we observe in the Acheulian—long-term stasis coupled with short-term and localized outbreaks of novel behaviors that fail to become fixed in behavioral repertoires over extended time periods and spatial extents. The feedback between local behaviors, including stone tool fabrication practices, and the wider regional behavioral and developmental package of which they were a part, was weak, so the demonstrable small-scale innovative variability in the Acheulian had little or no long-term effect on its overarching character and did not drive directional change.

HOMININ LIFE HISTORIES AND THE GENERATION OF INNOVATION

If metapopulation ecology can illuminate the processes of innovation transfer *between* local hominin populations in the Middle Pleistocene, then a consideration of life history parameters can inform our understanding of the processes of innovation generation, adoption, and rejection *within* a local band. If it is assumed that the skills and knowledge that underpin the Acheulian tool kit were acquired by naïve young individuals through imitation and emulation (Petraglia et al. 2005), then the mechanisms of social learning are critical. The strength and direction of channels of transmission would have been key influences on the propensity for innovative behavioral change to arise and be locally adopted. One might assume that a preponderance of horizontal peer-to-peer transmission encourages greater behavioral variation and innovation, especially within cliques of children and adolescents, than a reliance on vertical adult-to-child/adolescent transmission. If so, then the apparent stasis of the Acheulian might suggest that there was a strong bias towards transmission from adults to the young. However, this would be rather simplistic. Group size, social structure, and the social and economic benefits of conformity must all be considered.

Human life history can be divided into five stages—the infant (birth to weaning), the child (weaning to eruption of M1), the juvenile (from M1 to puberty and the onset of the adolescent growth spurt), the adolescent (from the onset of the adolescent growth spurt to the cessation of growth and maturation), and the adult. The childhood and adolescence stages are unique to humans (Bogin 2003; Kennedy 2003). Childhood conveys three specific advantages. First, the development of a childhood stage coincides with a shortening of the infancy period during which mothers are lactating, meaning that they more quickly become fertile again and can sustain shorter inter-birth intervals (Aiello and Key 2002; Bogin 2003). Second, 'the human childhood stage adds an additional four years of relatively slow growth and allows for behavioral experience that further enhances developmental plasticity' (Bogin 2003: 32). Similarly, Kaplan et al. (2000) argue that adolescence provides additional years of development that enable hominins to 'learn and practice technology, social organization, language and other aspects of culture' (Bogin 2003: 32). Finally, in mammals that exhibit juvenile phases, a greater percentage of offspring reach adulthood than in species without this stage. Accordingly, it is believed that the childhood and adolescence stages dramatically enhance offspring survival.

There is general consensus that the life histories of late Lower and early Middle Pleistocene *Homo* included either a childhood stage for the first time or a significantly expanded childhood (Bogin 2003; Krovitz et al. 2003). Skeletal evidence points to an adolescence stage for early *Homo sapiens* (Antón and Leigh 2003; Bogin 2003) although opinion is divided over whether or not this stage was part of the life history of *Homo erectus sensu lato* (Antón and Leigh 2003; Bogin 2003; Tardieu 1998). This is very important because the appearance of extended childhood, and possibly adolescence, life history phases implies that there was additional time to learn social, ecological, and technical skills, and extensions in those parts of the life cycle during which individuals are most open to acquiring novel skills.

The duration of childhood and adolescence may, however, have been considerably shorter in Acheulian hominins than in later humans (Nowell in press) since they seem to have experienced a faster pace of ontogenetic development than did early and living *Homo sapiens* and, probably, Neanderthals (Dean et al. 1986, 2001; Nowell in press; Smith et al. 2007, 2010). If childhood and/or adolescence in *Homo erectus sensu lato* was significantly shorter than in later humans, then it follows that the propensity of individuals to learn and devise novel behaviors would be relatively reduced. The very idea of the handaxe, and the bodily skills and technical routines required for its production, were probably habituated and imprinted in a relatively constricted early learning process. Consequently, a short childhood in small groups with limited numbers of models to emulate and imitate, and of peers with whom to play and experiment, would limit the cognitive and social room for innovation. The constriction of those life history phases in which novelty, experiment, and innovation are most readily embraced would therefore inhibit the likelihood of novel behaviors arising and being locally adopted. Furthermore, it may also be that there were competing pressures to 'use this time' in other ways. Bogin (2003: 38), for instance, argues that 'adolescence became part of human life history because it conferred significant reproductive advantages to our species, in part by allowing the adolescent to socially integrate into the economic, sexual and political world of adults [and to] practice [these] behaviors before reproducing.'

If so, then then our stereotype of adolescent rebellion could be clouding our judgment. Indeed, one implication of Bogin's view is that, in late Lower and early Middle Pleistocene hominins, the adolescent phase was a 'rite of passage' into society involving the development of full relational and economic roles, rather than a period during which individuals were free to participate in culturally deviant groups. From that perspective, innovativeness could have amounted to 'cultural delinquency' and was probably detrimental to fitness. Combining this idea with the small, intimate and effective social networks in which Gamble (1999) envisages Lower Paleolithic hominins to have lived—where daily contact is only with kith, kin, and taskmates—then it might be that everyday elaborations on existing themes to serve immediate purposes and the refinement of already-acquired skills as a part of adolescent social maneuvering, were the most appropriate strategies for young hominins. Indeed, such a viewpoint is consistent with recent studies that emphasize how Paleolithic technology was not merely an instrumental procedure for the achievement of material goals, but was instead socially active and inherent in the ongoing negotiation, production, and reproduction of individual and social being and identity (Dobres 2000; Gamble 1998, 1999). As Gamble reminds us, the object itself need not assume any overt symbolic meaning outside its original context for the performance of its making to have this social power. In the act of producing a handaxe, Acheulian children and adolescents also were reproducing their own society and, in such small and vulnerable populations, we should not expect them to have been routinely subversive of conventional technological practices or behaviors.

THE TRANSITION TO THE MIDDLE PALEOLITHIC/MIDDLE STONE AGE

Thus far we have focused on explaining how local and short-term innovativeness coexisted with global long-term stasis in the Acheulian. We have also noted how some innovative aspects of the Acheulian, and especially the occurrence of PCTs, anticipate the Middle Paleolithic and Middle Stone Age. Indeed, as we have suggested, the model illuminates that transition. Evidence, primarily from histological analysis of dental remains, suggests that both Eurasian Neanderthals and African early *Homo sapiens* exhibited delayed maturation, and therefore extended pre-adult life history phases in which the capacity to learn and innovate is at its greatest (Dean et al. 1986, 2001; Nowell in press; Smith et al. 2007, 2010; but see Hawcroft and Dennell 2000, and Ramirez Rozzi and Bermudez de Castro 2004, for contrary views with respect to Neanderthal maturation rates). The increase in hominin endocranial capacities from 300 kya implies an increase in local population size (Aiello and Dunbar 1993; Aiello and Wheeler 1995; Ruff et al. 1997). Greater raw material displacement distances and the first systematic occupations of mountainous landscapes and of highly seasonal environments in eastern Europe and central Asia in the Middle Paleolithic (Féblot-Augustins 1997a, 1997b; Hopkinson 2007a, 2007b) strongly suggest an expansion of foraging ranges. From 300 kya, factors promoting both the within-group generation of innovations, and their transmission through and retention in metapopulation-level behavioral repertoires, were in place. This accounts for the observed pattern—that innovations such as PCTs which remained localized and ephemeral in the Acheulian, subsequently became enduring and widespread components of hominin behavior.

The significance of this goes beyond the post-Acheulian proliferation of prepared core technologies. It is widely recognized that, in the African Middle Stone Age, innovative behaviors (e.g., the use of grindstones and pigments, microlithic technologies, regionally specific artifact style, the effective exploitation of marine and aquatic resources, symbolic material culture) developed cumulatively and coalesced into a 'modern' package by around 50 kya (Klein 2008: Table 1; McBrearty and Brooks 2000). It is also now becoming clear that, despite a long-standing conviction that the Eurasian Middle Paleolithic was, by contrast, static and conservative (e.g., McBrearty and Brooks 2000; Mellars 1973), it was in fact a period of cumulative behavioral development. Middle Paleolithic stone artifact industries exhibit time-vectored change both within and between regions (e.g., Delanges and Meignen 2006; Hovers and Belfer-Cohen 2006). Game species specialization (Grayson and Delpech 2002, 2008), the systematic exploitation of marine resources (Cortés-Sánchez et al. 2011; Stringer et al. 2008), fowling (Blasco and Fernández Peris 2009), controlled pyrotechnology (Courty et al. 2012; Daniau et al. 2010; Goldberg et al. 2012; Roebroeks and Villa 2011), and the production of symbolic material culture (Morin and Laroulandie 2012; Peresani et al. 2011; Zilhão et al. 2010) are all now documented in European Middle Paleolithic contexts. The Eurasian Middle Paleolithic, like the African Middle Stone Age, was a period in which the generation and accumulation of innovations exceeded that of the Acheulian by an order of magnitude.

Yet it is also apparent that this was not a linear process. In both Africa and Eurasia between 300 and 40 kya, innovative behaviors could be, and were, lost. The barbed bone harpoons from Katanda (Yellen et al. 1995) and the Howiesons Poort phenomenon (Soriano et al. 2007) are African cases in point. In the Eurasian Middle Palaeolithic, the examples of subsistence fowling and controlled pyrotechnology cited above are occasional, not typical, features of the archaeological record. In most of Europe, the terminal Middle Paleolithic tends to be dominated by discoidal technologies and naturally backed pieces, and lacks the relatively formalized and regionally-specific bifacial components (e.g., foliates, *Keilmesser*, cordiform and *bout coupé* handaxes) typical of the immediately preceding period. Of course, that is precisely the pattern our model would expect if there were any variations in life history, demographic, or metapopulation parameters in the Middle Stone Age and Middle Paleolithic. Local and regional extinctions and population crashes driven by events such as the Mount Toba eruption (Ambrose 1998) or glacial-interglacial cycles (Hublin and Roebroeks 2009), together with low effective population size and increased birth intervals, at least among Neanderthals (e.g., Briggs et al. 2009; Lalueza-Fox et al. 2011, 2012) would all, in the terms outlined here, have the effect of weakening the cultural transmission of skills and practices in time and space. Indeed, isolation and population decline had an identical effect even in Holocene Tasmania (Henrich 2004).

DISCUSSION

This exploration of the consequences of life history parameters and of the relations between demographic, social, and ecological dynamics at local population and metapopulation scales demonstrates that the apparently paradoxical nature of the Acheulian is not in fact paradoxical at all. Indeed, the coexistence of local, short-term novelty and global long-term stasis is a predictable property of a hominin lifeway predicated on a life history organized into distinctively human phases, but with reduced childhood, juvenile, and adolescence stages, and on social life lived in small, thinly distributed local populations with limited foraging ranges and inter-population migration.

Of course, the stiffest methodological challenge lies in deriving robust estimates of the relevant variables, with sufficient chronological resolution, from archaeological and fossil traces. The Lower and Middle Pleistocene hominin fossil record is sparse, and the archaeology of the Acheulian is dominated by assemblages derived from secondary depositional contexts. The derivation of hominin group sizes from endocranial volumes (Aiello and Dunbar 1993) is not clear cut or straightforward; for example, Steele (1996) has criticized such attempts on the basis that the relationship between endocranial capacity and neocortex size is complex, and that a significant proportion of variability in primate group size cannot be explained by brain size. Similarly, mathematical modeling developed by Brantingham (2006) has cast doubt on any simple relationship between raw material displacements and hunter-gatherer foraging ranges. Factors such as planning depth, risk management, and raw material quality and abundance can impact upon raw material displacements in forager mobility strategies without any necessary change in foraging range. It should also be recognized that the study of Lower and Middle Pleistocene hominins is currently denied the genomic data that might cast light on population history, local group size (Lalueza-Fox et al. 2011), and possibly maturation rates (Smith et al. 2010: 20926).

Nevertheless we contend that the systematic increase in raw material displacements across the Lower-Middle Paleolithic transition in Europe, together with the incorporation of uplands and lowlands into integrated mobility strategies and the systematic eastward expansion of Middle Paleolithic settlement into central Asia (Hopkinson 2007a), necessarily imply some permutation of larger local population sizes, increased local population packing densities, and extended mobility ranges (though not necessarily the same permutation at all Middle Paleolithic times and places). The association of those developments with a trend towards the accumulation of behavioral novelty can be taken as a broad validation of the model.

At the same time, further advances need to be made for a life history-metapopulation model to be more completely operationalized. The length of hominin pre-adult life history stages, for example, are in principle resolvable through the further development of methodologies for understanding hominin ontogeny from the histological analysis of dental remains. Perhaps the most challenging problem methodologically, in the light of Steele's criticisms, is the robust estimation of hominin local group sizes. Here we are handicapped not only by the absence of genomic evidence for the Lower and Middle Pleistocene, but also by the secondary depositional contexts that dominate Acheulian archaeology, and which preclude methodologies for inferring changes in Paleolithic population levels from archaeological evidence (e.g., Mellars and French 2011). It should be emphasized, though, that these problems are no more intractable than demonstrating evolutionary developments in the organization of the brain in support of conventional cognitive explanations for the character of the Acheulian.

SUMMARY AND CONCLUSION

During the Middle Pleistocene certain life history parameters of archaic hominins approached those of modern humans. Despite this, the Acheulian and contemporaneous technological systems were remarkably 'unmodern' in being static over long periods of time and wide geographical areas. We suggest that this stasis conceals higher levels of short-term, localized variation and inventiveness than have hitherto been generally recognized, but that innovation in the Acheulian was weak in that novelty was unable to persist and disseminate much beyond the realm of the short-lived local population or band. We suggest that explanations of this predicated on cognitive or linguistic deficiencies are insufficient to explain what should be seen as a social or socio-economic question. Ultimately then, we hope that the continued quest to understand why the Acheulian remained static for so long may help us understand more about the social lives and learning environments of archaic hominins.

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ENDNOTE

1. This differs from Renfrew's (1978: 89–90) usage of the terms, in which 'invention' refers to the generation of novelty by individuals, and 'innovation' to its social introduction and development.

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