The Seasonality Thermostat: Female Reproductive Synchrony and Male Behavior in Monkeys, Neanderthals, and Modern Humans

CAMILLA POWER
Anthropology Programme, School of Law and Social Sciences, University of East London, 4–6 University Way, London E16 2RD, UNITED KINGDOM; c.c.power@uel.ac.uk

VOLKER SOMMER
Department of Anthropology, University College London, Gower Street, London WC1E 6BT, UNITED KINGDOM; v.sommer@ucl.ac.uk

IAN WATTS
20 Aristophanous, Psirri, Athens 105 54, GREECE; ochrewatts@hotmail.com

ABSTRACT

Reproductive synchrony or desynchrony of primate females influences number and fitness of males in mating systems. Langur monkey populations provide a natural experiment for observing alternative female strategies of confusing or concentrating paternity. Where females escape seasonal reproductive constraints, they desynchronize fertility and show visible cues (menstruation), enabling single males to monopolize matings. This increases female fitness by reducing food competition. Where langurs are seasonally constrained, females conceal fertility, confusing paternity and reducing infanticide. These case studies illuminate how hominin females could increase male numbers and investment. Fitness payoffs to male investors will be affected by degree of reproductive seasonal constraint, and by females either concealing or confusing menstrual cues of imminent fertility. Among ancestors of modern humans and Neanderthals these strategies diverged. Under pressure of encephalization, modern human female ancestors, less seasonally constrained, pursued a strategy of cosmeticization of menstrual signals. This Female Cosmetic Coalitions model accounts for the African Middle Stone Age record of pigment use. Among Neanderthals, strategies alternated. Severe seasonality during glacial cycles tied Neanderthal males into pair-bonds, suppressing cosmetic signaling. Only during interglacials when seasonality relaxed would Neanderthal females require blood-red cosmetics. Our Seasonality Thermostat model explains why European ochre use correlates with climate through the Middle to Late Pleistocene.

INTRODUCTION

There is a growing consensus that evolving *Homo* mothers relied on cooperative breeding to raise larger-bodied, larger-brained offspring (e.g., Aiello and Key 2002; Barrickman et al. 2008; Burkart et al. 2009; Hrdy 2009; Robson and Wood 2008; Shultz et al. 2012; van Schaik et al. 2006). But many questions about pathways and mechanisms remain open. For example, who were the original providers of allocare—older female kin (Hawkes et al. 1998; O'Connell et al. 1999), mates (Kaplan et al. 2000), or a combination of both (Aiello and Key 2002; Opie and Power 2008)? Even given probable 'grandmother' support, there is little doubt that during the evolution from early *H. erectus* (twice the brain size of chimpanzees) to *H. heidelbergensis* (over three times chimpanzee brain size), male support of female reproduction increased significantly. But was male investment kick-started by mating or parental effort (Trivers 1985)?

Models for cultural levels of human cooperation (Boyd and Richerson 1992, 2002, 2005; Gintis et al. 2003; Henrich and Boyd 2001; Henrich et al. 2003, 2006; Nowak and Sigmund 2005; Richerson et al. 2003), invoke multilevel and group selection processes, but ignore what is most difficult to explain—how to secure cooperation between the sexes, given the trade-off between investing in current offspring versus future mating opportunities (cf. Bowles 2006). One game theory model (Key 1998, 2000) incorporated the differences of reproductive energetic costs to specify conditions for the evolution of cooperation that can be practically applied to the fossil record. Yet even these conditions do not identify how females induced males to subsidize their reproduction (Kaplan et al. 2000; Marlowe 2001). Recent models (Gavrilets 2012) highlight the difficulty of shifting from systems of significant male mating competition into productive male investment, where males face a social dilemma of ceding fitness advantage to free-riding rivals.

If we can define the mechanisms available to *Homo* females giving them leverage against male defection through the Early to Middle Pleistocene, we will have a much improved grasp of the evolution of social and economic exchange. In particular we may be able to address questions of different behavioral outcomes in the sister lineages of Neanderthals and our own African ancestors. Archaeologists (Macdonald et al. 2009; Roebroeks and Verpoorte 2009) have begun to investigate the implications of differ-

PaleoAnthropology 2013: 33−60. ISSN 1545-0031
doi:10.4207/PA.2013.ART79

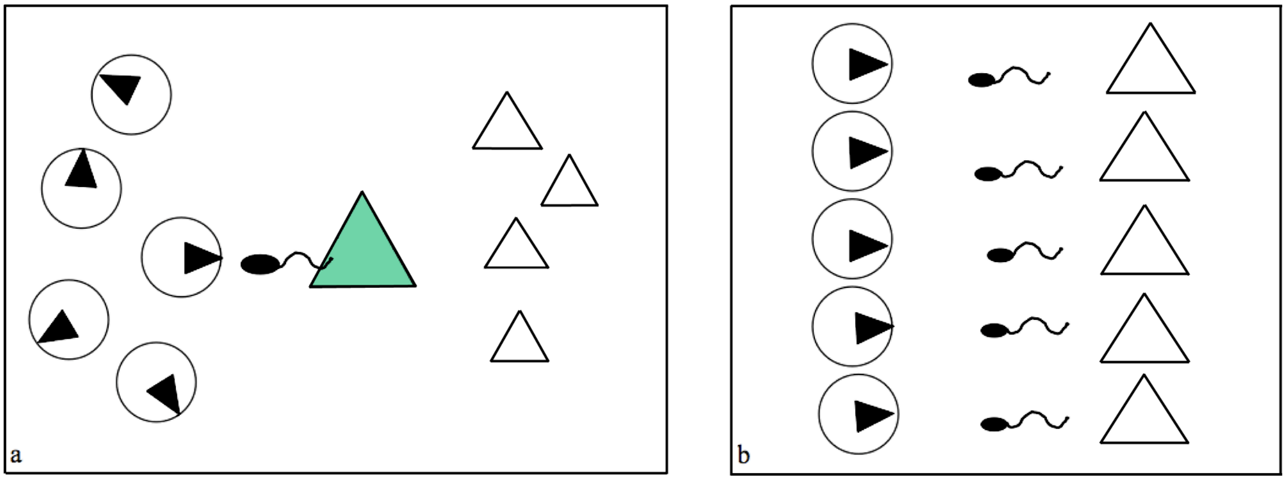

Figure 1. Model of effects of reproductive synchrony in social primates: a) where females do not synchronize, dominant male guards the harem; b) if a critical threshold of females synchronize, lower-rank males will invade to access unguarded females while the dominant male is occupied.

ences between Neanderthals and moderns human energetic requirements; how these impacted on female reproductive strategies still has to be explored (but see Mussi 2007).

The broad context of primate mating systems suggests females can alter male behavior via sexual signals. This could occur either through giving, confusing, or concealing information regarding current state of fertility (Hrdy 1981; van Schaik et al. 2000), or through differing degrees of synchrony or desynchrony in reproduction (Ostner et al. 2008). Alterations in these parameters change male payoffs for supporting or deserting mates; they also affect the distribution of mating opportunities, and chances of monopolization for any male. These aspects of sexual competition would be critical to overall increases of male investment. Machiavellian intelligence models for the emergence of egalitarianism in hunter-gatherers have highlighted economic counter-dominance mechanisms (Boehm 2001; Erdal and Whiten 1996). Yet, from an evolutionary perspective, the most critical aspect of counter-dominance must be the leveling of reproductive opportunities among males (Bowles 2006; Whiten and Erdal 2012) as this will tend to increase the average economic support females may gain.

Our paper draws on nonhuman primate data on female reproductive synchrony versus desynchrony, and the effects on parameters such as operational sex ratio (defined as the average ratio of fertilizable females to sexually active males at any given moment [Emlen and Oring 1977]), paternity confusion or concentration, lesser or greater risks of infanticide, and the influence of male presence or absence on food availability, and, ultimately, birth rates. We will examine the interaction of these variables in case studies of langur monkeys, given that natural populations of these monkeys show a high degree of flexibility in their reproductive patterns. These can provide insights to inform models of hominin evolution. There are serious differences, of course, between catarrhine monkeys and hominin ancestors—most notably males compete for food with females among the monkeys, while among *Homo* ancestors they became net providers. But, the basic mechanisms of synchrony or not, visibility of sexual signals or not, may have similar influence on continued presence or absence of males, in both langurs and *Homo* spp. Investigating langur female strategies, and the effect on males, will lead us to predictions concerning *Homo* spp. which are testable in the archaeological and paleoclimate records. This may allow us to understand differences in cultural strategies between Neanderthals and our ancestors.

THEORY OF SYNCHRONY: PRIMATE EXAMPLES

In mammalian mating systems generally, and among primates in particular, female spatio-temporal distribution—how clumped females are in the environment and how much they overlap their fertile periods—affects male ability to monopolize matings (Clutton-Brock 1989; Emlen and Oring 1977). The basic principle is, the more females are fertile simultaneously, the less likely it is that any single male can fertilize all of them, therefore more males (usually lower-ranked) come into the breeding system to attempt to access those 'free' females (Figure 1).

The number of males in a group is therefore influenced by the number of females and their degree of reproductive synchrony, although it may be difficult to distinguish between these effects since the more females there are, the more likely is some overlap (Nunn 1999). Moreover, the degree of seasonality in reproduction is a good predictor of whether groups contain single or multiple adult males (Ridley 1986, but see Mitani et al. 1996). Significant seasonality increases the probability that females overlap their fertile periods while it decreases the likelihood that any single male can guard and impregnate a whole group of females. Once the number of co-cycling females rises above a critical threshold (Dunbar 1988: 140–143), a harem-holder may be unable to prevent other males from invading and mating with his females.

Seasonal variation of day-length, temperature, or rainfall influences food availability and hence timing of reproduction (Bronson 1988; Sadleier 1969). Environmental constraints of seasonal synchrony may in fact be costly for females if more males eat into their food supply.

Females could also use synchrony facultatively to affect numbers of males, with potential benefits of reduction of infanticide (van Schaik et al. 1999). Undermining male monopoly and spreading chances of paternity among several males can give females more protection. More males can also offer protection from predation (van Schaik and Heistermann 1994). Of further possible benefit to females are increased levels of male care. Primate species living in temperate zones, which tend to be more seasonal, show more male investment, especially infant-carrying, relative to tropical species (Cichy 1997; Cichy and Ford, cited by Burne 1995), even where females mate more than one male. The more even operational sex ratio in seasonal species allows lower-ranked males more mating opportunities, and these males may be most inclined to offer care such as carrying when the benefits to infants and mothers are greatest, for instance during harsher seasons (Anderson 1992).

Female reproductive synchrony should also considerably influence male reproductive success (RS), in terms of reproductive skew—the degree to which a dominant animal monopolizes fitness. In a study of 12 primate species, mostly macaques, breeding seasonality was found "to be one of the most important variables affecting the relationship between rank and RS in non-human male primates" (Paul 1997: 344). However, phylogenetic comparative tests across 31 species assessing the effect on male skew of female reproductive traits, including breeding season duration, oestrus duration, and degree of oestrous overlap, did not support such an effect (Kutsukake and Nunn 2006). The authors suggest this may be because their sample included only multimale species. They point to long-term data on chimpanzees where an increased number of synchronously receptive females decisively altered the relative success of the alpha and beta males (Boesch et al. 2006: Figure 4). In this case, where under two females were in oestrus together, the top male took nearly 90% of fitness, the second 0%, less than the third-ranked. When over two females synchronized oestrus, the fitness among all three top rank males virtually equalized at 30%. In a metaanalysis of 27 studies of 19 primate species, female oestrous synchrony was confirmed as the main predictor of male paternity distribution (Ostner et al. 2008). A recent study of 71 species with a broader range of strepsirrhine and haplorhine taxa (Carnes et al. 2011) confirmed that female reproductive synchrony affects male ability to monopolize matings. Oestrous synchrony had the major effect, followed by birth seasonality and then breeding season duration. Again, the fundamental principle is, the more females synchronize (at oestrous cycle level or at seasonal level), the less any dominant male can monopolize fitness.

Strong breeding seasonality or reproductive synchrony is certainly effective in spreading the chances of paternity among more males. Combined with concealment of ovulation and/or extended oestrus with unpredictable ovulation, it is one of the mechanisms that allows females to simultaneously concentrate and confuse paternity, awarding each male chances of paternity that are optimal from the female's perspective (van Schaik et al. 2000: 363).

ADJUSTING SEXUAL SIGNALS: THE CASE OF LANGUR MONKEYS

The reproductive parameters of monkeys and apes such as length of gestation, menstrual cycles, and periods of receptivity exhibit a certain degree of intra-specific variability. Such fluctuation typically reflects constraints imposed by the environment that force females to make the best of a given situation. Actual female preferences might be difficult to elucidate, for example, with respect to the temporal patterning of fertility in relation to group mates.

However, observations on a species of colobine monkey, the Hanuman or Grey langur (*Semnopithecus [Presbytis] entellus*), offer a unique opportunity to assess strategic decision-making by female primates. This possibility arises through long-term data collected on two populations that live under extremely different environmental conditions (Koenig and Borries 2001). The reproduction of one population is highly seasonal, whereas the other produces offspring throughout the year. Seasonal reproduction is forced upon the females through dramatic alternation between wet and dry seasons with corresponding fluctuations in food availability. The pattern of continual reproduction, on the other hand, is the result of crop-raiding and food provisioning by local Hindu people (Sommer 1996), which offsets natural environmental constraints. This allows an 'experiment' of removing seasonal food limits. As a result, we can observe how female fertility is patterned under constrained conditions, and how females alter their reproductive parameters if such constraints are lifted—thus reflecting their strategic choice.

Hanuman langurs are colobine primates, which inhabit diverse habitats across the Indian subcontinent, including mountains ranges, flood plains, semi-arid zones, deciduous or evergreen forests, and urban landscapes. They thrive on a diet that consists mainly of leaves, herbs, seeds, and fruit, and may survive for months by consuming mainly mature leaves. Langurs are flexible both ecologically and in their social organization. In some areas, langurs form multi-female/multi-male troops. Elsewhere, multi-female/one-male troops correspond with all-male bands formed by males excluded from troops. In other places, varying proportions of both systems occur simultaneously. The balance of one-male versus multi-male social organization reflects corresponding differences in reproductive physiology and, as a corollary, in social behavior.

The general reproductive pattern varies with food availability. As a rule, births are restricted to 3–5 months per year in more northern populations, whereas this seasonality is less expressed in other parts of India and in Sri Lanka. As mentioned, some populations are practically non-seasonal because crop-raiding and provisioning sustains females through periods of shortages in the availability of natural foods.

In accordance with the primate models of synchrony discussed above, degree of seasonal reproduction determines why some populations form one-male groups and others multi-male—as even the strongest male cannot monopolize a group of females against competitors when several of them are fertile at the same time (Srivastava and Dunbar 1996). This is, because whenever a male mates with one female, he cannot effectively guard the others. Reproductive synchrony thus facilitates the development of multi-male groups. In a non-seasonal population, by contrast, only one or two females might be fertile on any given day, allowing prime males to effectively exclude access for competitors.

Females in one-male troops cooperate closely, for example, with respect to home range defense, fending off aggression of non-resident males, and by sharing infants through a system of baby-sitting (Sommer 1989). In contrast, little cooperation occurs between adult males, whether they are members of all-male bands or troop residents. Genetic relatedness influences these behaviors (Little et al. 2002). Infants sired during the tenure of a single male are at least paternal half-siblings. Troop females are closely related, since females are philopatric and remain in their natal group. Members of all-male bands, on the other hand, are generally unrelated, bands being made up from various cohorts of expelled bachelors (Rajpurohit and Sommer 1993) and having high levels of turnover. The balance of cooperation and competition thus reflects the forces of kin selection.

Immigrant males in one-male/multi-female troops tend to kill infants sired by their predecessors (Sommer 1994). Such infanticide shortens the temporary sterility of females associated with lactation and increases a male's chance to reproduce. Far fewer infanticidal events occur in multi-male/multi-female troops (Borries et al. 1999a). This is partly because infanticidal males will have to wait until the next mating season before they can fertilize a female whose infant they killed, removing the incentives for such killings. However, if weaning takes place when infants are much older than one year, then it still pays to remove them, as this extended maternal investment correlates with interbirth intervals of 2–3 years.

Females seem to be able to reduce infanticide rates in multi-male societies through copulation with various males. A male who mated with a particular female will be reluctant to harm her offspring, given the chance that he might have sired the offspring. This mechanism of paternity confusion reflects the fact that it is costlier for males to kill their own offspring by accident than to not harm a competitor's baby. Even a slight chance of paternity can therefore prevent infanticide (Ostner et al. 2006).

The possibility of using sexual behavior as a means to manipulate male behavior is enabled in langur females because they do not show sexual swellings around the time of ovulation—unlike, for example, some macaques, baboons, or apes. However, the ovulatory period is still distinct, but instead marked by high rates of female solicitation for sex, based on gestures such as head-shuddering, presenting of the ano-genital region, and lowering of the tail. The dynamics of these general factors translate into a particular patterning of female reproductive parameters under the conditions of extreme birth seasonality or non-seasonality.

The seasonal population in question lives near the village of Ramnagar in southern Nepal's Chitwan District (Koenig et al. 1997). Here, at an altitude of 300m, langurs live in a semi-evergreen forest dominated by the dipterocarp Sal tree (*Shorea robusta*). The climate is characterized by a hot, wet summer from May to September, with temperatures of up to 43°C and an annual average rainfall of 2,279mm. This monsoon region coincides with fruiting and flushing of major food plants, whereas plant food is markedly scarce during other times of the year. In Nepal, in contrast to India, langurs are not considered sacred, so Ramnagar langurs are not provisioned and crop-raiding has not been observed. As a consequence, reproduction is seasonal, with conceptions occurring between July to November, and the majority of births taking place between February and May. Langurs live at a moderate density of 26 individuals per km^2 in largely overlapping home ranges. Groups are typically multi-female/multi-male groups containing on average 18.3 individuals, with about one adult male for every four adult females and her offspring.

Infanticide occurs once in 2.5 group years (Koenig and Borries 2001); this may seem like a low frequency. But, the Ramnagar population reproduces very slowly, with a mean birth interval of 2.4 years. Thus, overall, 15–17% of all liveborn infants die by infanticide, and 31–33% of unweaned infants. Females have significantly longer interbirth intervals if infants survive weaning. Most attackers are residents of the infants' groups who had immigrated after the infants had been conceived or born. As non-resident males sire 21% of the infants, recent immigrants might risk killing their own offspring. Genetic data, however, confirmed that males attacked or killed only infants they had not sired and that presumed killers were the likely fathers of subsequent infants. These findings strongly support the sexual selection hypothesis of male-committed infanticide.

The non-seasonal population lives in the vicinity of the town of Jodhpur, located in Northwest India in the state of Rajasthan (Rajpurohit et al. 1995; Sommer 1996). Here the climate is dry, with temperatures fluctuating between 0°C and 50°C. Rain averages just 360mm of which 90% falls during the summer monsoon. A hilly sandstone plateau on which the town is erected covers about 85km^2 and is inhabited by a geographically isolated population of langurs. Water is available year-round from artificial ponds. Apart from feral dogs, natural predators are absent. All monkeys forage on the xerophytic open scrub vegetation and some groups raid crops (Sommer and Mendoza-Granados 1995). Additionally, most monkeys are provisioned by local people with high-quality food such as wheat or millet cakes, sweets, fruits, or vegetables, amounting to 16–33% of their feeding time. In correspondence with an increase in the urban human population, the langur population grew from

1,300 to about 3,000 between 1967 and 2000.

Births occur year-round and rates are evenly distributed across 10 of 12 months, with only a discernible peak in March and a maximum in November (Sommer et al. 1992). The mean interbirth interval is 17.2 months. The reproductive units are 27–29 multi-female/one-male troops which average 38.5 members (range 7–93) occupying home ranges of 0.5–1.3km². Females are philopatric. Maturing males emigrate into one of 12–14 bands which average 11.8 members (range 2–47) (Rajpurohit and Sommer 1993; Rajpurohit et al. 1995). They roam through habitats of 1.5–3.5 km² which are often low-quality. Residencies of single adult males last from a few days to 74.0 months, on average 26.5 months (Sommer and Rajpurohit 1989). Stable one-male situations are typical for 94.5% of a given troop's history. Male bands invade troops in an unpredictable pattern, which may result in rapid or gradual changes of the respective harem holders. One-third (34%) of all infants present during male take-overs are killed through infanticide, and many more are attacked. This translates into a rate of 14% of all liveborn infants being killed by infanticide (Borries and Koenig 2000), a figure similar to that for multi-male/multi-female troops. However, given that birth intervals are much shorter, females living in one-male troops experience infanticide about 40% more frequently and are estimated to lose 22% of their offspring to infanticide throughout their lifetime (Sommer 1994).

A comparison between the Ramnagar and Jodhpur populations reveals how females can manipulate male behavior to a certain degree.

In a multi-male/multi-female setting, it could be advantageous to confuse paternity and achieve a corresponding reduction in infanticide risk. Under such conditions, it is expected that females withhold information that would allow males to estimate when ovulation occurs. Cycling females should therefore suppress visible sign of menstruation, since this indicates the onset of the follicular phase, while at the same time extending the peri-ovulatory window when they display receptive behaviors. This strategy can, however, only work if males are unable to detect the exact date of ovulation.

The existence of such a mechanism has indeed been confirmed for the Ramnagar population (Ziegler et al. 2000; Heistermann et al. 2001). Here, menstrual bleedings are not visible. Moreover, rates of copulations, anogenital inspections, and consortships indicate that, while males are able to generally distinguish between females that are fertile (i.e., cycling) and non-fertile (i.e., pregnant or lactating) (Ostner et al. 2006), they are unable to pin-point the exact date of ovulation (Ziegler et al. 2000). Females are receptive during 34.1% of all cycle days, i.e., for an average of 9.2 days during cycles that last on average 27.0 days. The length of the monthly receptive period can vary from 4–15 days. Hormonal analyses based on fecal samples revealed that ovulation can occur on the first, the last, or any intermediate day of the receptive period. Importantly, female attractivity as measured through copulation rates did not vary, and neither did the likelihood that a high-ranking male would monopolize females on the day of ovulation. As a result, paternity data based on fecal samples reveal that males of various social standings sire offspring. While the dominant male sires 57%, other resident males sire 22% and outside males 21% (Launhardt et al. 2001). In extension, male behavior is shaped by whether or not they copulated with a given female around the time of conception. Males that did will protect a resulting offspring against attackers—independently of whether or not they were the actual sire or just a non-fathering copulator. Vice versa, attackers of infants had invariably not mated prior to conception (Borries et al. 1999b). The Ramnagar data therefore clearly demonstrate how female sexuality influences the pattern of male investment.

Could females do better if they lost their synchrony, thus facilitating a single male to control them against competitors? Theoretically, this would be advantageous because such a system would strongly reduce food competition from adolescent and adult males which, in turn, should shorten birth intervals. Such an option, however, is not normally open to females given that the seasonality of the environment forces them to synchronize their fertility.

Nevertheless, the quasi-experimental situation in the Jodhpur population where local people tolerate crop-raiding and provide monkeys with food allows us to test these assumptions. At this site, females are basically presented with a choice. They *could* still synchronize their cycles. But, the data show that they do not. In fact, females desynchronize their periods of receptivity to a degree that is close to the mathematically possible optimum (Alberts 2006). As a result, troops are virtually always one-male, and females do not have to compete with multiple males for food. One might wonder why this should happen in the first place, given that locals provision the monkeys. But, females are always outcompeted by adult males when food is provided or when monkeys raid crops. In both situations, food items are highly clumped, and males will eat them at the expense of females.

We can also predict that females should provide harem residents with clues that assure them of paternity of their subsequent infant, to increase protection against the threat of incoming males. Jodhpur females appear to alter their reproductive parameters in three ways (Sommer et al. 1992). Firstly, menstruations as a sign of impending fertility are clearly visible to human observers in 89% of all cycles, lasting for an average of 1.9 days (range 1–6 days)—as opposed to being invisible in the multi-male society of Ramnagar. Secondly, menstrual cycles at Jodhpur last only 24.1 days on average and are thus 3.9 days shorter than at Ramnagar. Thirdly, the receptive period is much contracted, lasting only 4.0 days (range 1–12), with receptive days thus making up only 16.6% of an average cycle—compared to 34.1% of all days at Ramnagar. As a result, paternity certainty is all but ensured for harem holders at Jodhpur, and they are therefore literally willing to fight to the death to protect their progeny (Rajpurohit et al. 1995). Moreover, interbirth intervals last on average only 1.4 years—almost halving the 2.4 years observed at Ramnagar.

In conclusion, reproductive parameters in a primate such as Hanuman langur monkeys can strongly influence male behavior, and females seem to be proactive in making use of that tool, if they can. On the one hand, cycle synchrony results in paternity confusion and male investment. On the other hand, cycle asynchrony results in paternity certainty and high infanticide risk. Given a choice, females seem to prefer a higher rate of infant-killing associated with a one-male social system over lower infanticide rates in a multi-male system as this would come with an increased level of food-competition from males. This would lengthen birth intervals and would leave females, measured over a lifetime, with diminished reproductive success.

There is no reason to assume similar mechanisms would not shape the behavior of other primates, including humans. However, monkeys offer a more convenient model to unravel such dynamics.

HOMININ MODELS OF CONCEALED OVULATION, EXTENDED RECEPTIVITY, AND EFFECTS ON MALES

Could the variables which significantly influence mating and breeding in monkeys also have been effective in human evolution? Modern human females tend to extend sexual receptivity throughout the cycle, making it difficult for males to pinpoint ovulation (Baker and Bellis 1993: 880; Grammer 1996). Men may be able to distinguish between pre-ovulatory follicular and post-ovulatory luteal phases (Miller et al. 2007), but follicular phases vary so much in duration that ovulation is nevertheless highly unpredictable (Martin 1992). This feature is linked across primate taxa with selection for paternity manipulation (van Schaik et al. 2000: 384) and gives women increased ability to confuse paternity. It has been argued that the relatively continuous receptivity of modern females combined with concealed ovulation fosters pair-bonding and *greater* paternity certainty—if a male is forced to guard his female round the clock he can be reasonably sure her offspring is his (Alexander and Noonan 1979). An alternative hypothesis (Hrdy 1981) maintains that concealed ovulation with continuous receptivity evolved as a counter-infanticide strategy. Comparative phylogenetic methods (Sillén-Tullberg and Møller 1993) found that, among anthropoid primates, loss of visual ovulation signals virtually always evolved in multimale contexts, indicating counter-infanticide was its first cause. But once evolved, concealed ovulation may nevertheless promote longer term pair-bonds and, consequently, increase male investment.

The evidence of women's sexual signals today suggests a design similar to that of langurs for paternity manipulation. However, human reproductive energetics are very different from catarrhine monkeys in view of marked body and brain size change. Humans also differ in that while male langurs compete for food with females, human males have become net subsidizers of female reproduction (Kaplan et al. 2000). But the puzzle is how this could have happened, given an initial condition in which primate males provide little or no food. In the langur case, where females were not environmentally constrained, they appeared to adopt a strategy of reducing numbers of males to reduce feeding competition. In the case of *Homo* evolution, we predict female strategies for increasing numbers of males, to the extent that males became helpful in provisioning. Could they have used similar mechanisms of synchrony and sexual signals to enable them to do that?

The evolution of genus *Homo* from over 2 ma was marked by significant encephalization (de Miguel and Henneberg 2001; Shultz et al. 2012). According to the social brain hypothesis (Byrne and Whiten 1988; Dunbar 1992, 1998), this indicates they lived in progressively larger social networks. In increasingly complex multimale-multifemale social groups, it is probable that *Homo* females, even prior to *H. erectus*, had concealed and/or unpredictable ovulation with extended receptivity to reduce infanticide risk. Early African female *H. erectus* energetics of reproduction were drastically altered by body size change (Aiello and Key 2002). To maintain reproductive costs at a similar level to previous hominins, larger-bodied *H. erectus* females would have needed to shorten lactation, which implies that a female needed allocare for relatively early weanlings. Potential sources of extra investment were senior female kin (O'Connell et al. 1999; Voland et al. 2005), and/or mates (Aiello and Key 2002; Kaplan et al. 2000). In modeling the energetics of *H. erectus* reproduction, Opie and Power (2008) argue that mothers would have required support from both female kin *and* mates, implying a tendency to female philopatry by contrast with chimpanzees and bonobos. Given female energetic requirements, single-male harems were unlikely to be stable outcomes for *H. erectus*. A male who mate-guarded one or more females round the clock to ensure paternity would not be very productive; females are predicted to seek matings with more successful provisioners inclined to share high-quality foods. Evidence against harem organization is seen in reduced sexual size dimorphism in *H. erectus* relative to australopithecines, although this may have been driven by selection for larger female body size (McHenry 1996). Key and Aiello (1999, 2000) model increasing levels of male cooperation with females as an outcome of reduced body size dimorphism. Any single male was likely to be cooperative as an expression of short-term mating effort, but not necessarily reliable for the longer-term, if other mating chances came his way. Females could increase levels of investment by giving mating opportunities to more than one male—effectively the paternity confusion strategy—motivating them to offer mating effort in the form of provisioning. This would enable subordinate males to gain fitness in return for increased investment. The more females needed provisioning, the more they would be likely to reward these lower-ranked, more helpful 'investors'.

In early *H. erectus* social contexts, such investor males were more likely to compete for access with provisioning rather than try to secure increased paternity confidence since mate-guarding limits the ability to search for food (cf. Gilby et al. 2006, on how chimpanzee hunting productivity is undermined by mate-guarding of oestrous females).

From a female strategic viewpoint, she would be unlikely to let one male monopolize her when she had such a heavy reproductive burden. We therefore concur with the assessment of van Schaik et al. (2000: 386) that *Homo* females had an evolutionary heritage of paternity confusion, enabling avoidance of infanticide, with male support from mating effort, polyandrous mating and lack of exclusive pair-bonds. We are less persuaded that this operated in "strong patrilocal" contexts (2000: 387), given the need for cooperative breeding support from reliable female kin in addition to less reliable male mating effort (Hrdy 2009; O'Connell et al. 1999; Opie and Power 2008).

Concealed or unpredictable ovulation with more or less extended receptivity are features probably shared by langur and hominin females with the function of paternity confusion. But in the langur cases, other features had distinctive effects on the mating system—presence or absence of seasonality, and, presence or absence of menstrual signals. Seasonality determines numbers of males, while visibility of menstruation accompanies female desynchrony, enabling them to concentrate paternity on a single male. Although van Schaik et al. (2000) suggest human females have no evolutionary history of such paternity concentration, the high visibility of menstruation in *Homo* could cue males to imminently fertile females. We will now discuss how factors of seasonality and information from menstrual cues could affect *Homo* reproduction, potentially increasing amounts of investment extracted from males.

HOW MUCH CAN REPRODUCTIVE SYNCRHONY HELP *HOMO* FEMALES?

Turke (1984) first suggested that ovulatory synchrony and concealment combined with extended receptivity functioned in *Homo* ancestry to promote long consortship and ultimately pair-bonds. Turke used the model of Knowlton (1979) who considered synchrony as a strategy by the sex which invests most in offspring to secure greater parental investment from their mates. The greater the number of synchronized females, the less likely will a male be to gain fertile extra-pair matings before his own partner is once more ready to reproduce. So opportunity costs of paternal investment (in terms of extra-pair matings lost) may be outweighed by reproductive benefits accruing to paternal care (in terms of increased survivorship of offspring).

To synchronize fertility makes sense for encephalizing *Homo* females who need males to help out more with provisioning. However, Foley and Fitzgerald (1996) objected to Turke's scenario on the grounds that for hominins with interbirth intervals of 3–5 years, such synchrony was unrealistic. Infant mortality would disrupt synchrony since it would be too costly for a female who had lost an offspring to wait until the others started cycling again. Power et al. (1997) conceded it would be impossible to get clockwork synchrony throughout an interbirth interval, but argued that seasonal synchrony could still be effective in undermining male monopoly in *Homo*. If synchronized hominin females gave birth only on a 3-month time window in any year, a mother who lost an offspring need only wait a maximum of 11 months to conceive again. This cost can readily be offset by improved infant survivorship through extra male support, and environmental variation in food availability and energy budgets.

Still, seasonal synchrony falls short of bringing the one-to-one pair-bond sex ratios envisaged by Turke. If each female mated just one male per interbirth interval, it can guarantee only as many sexually active males as there are fecundable females in any breeding year. This lies between a quarter and a third of all breeding females assuming conditions of hominin evolution with interbirth intervals of 4–5 years, and some 25% infant mortality in the first year. Seasonal synchrony gives philanderer or dominant males fewer extra mating opportunities, and tends to reward males who stay longer to invest in females/offspring assuming that investor males gain payoffs of improved infant survivorship. Their mates may also have increased fertility as a result of extra male support. However, once impregnated, a female with 3–4 years until her next fertile cycles is liable to be deserted by any male when fertile females become available the following year.

As argued above, hominin females would be more likely to increase the ratio of male provisioning available per female by mating with more than one male each (Bellis and Baker 1990), spreading chances of paternity among multiple males. This would involve more males in the breeding system and further undermine dominant male monopoly of consortships. Chances of paternity rather than certainty are at issue here. A female is not concerned whether the male who offers provisions is the actual father of her offspring or not; while from a male viewpoint, if investment represents mating effort, that is, improving his chance of future sexual access, he is not concerned about the paternity of any specific offspring assuming he gains a probabilistic share of paternity.

Power (2001) modeled tipping points for philanderer males to adopt more faithful strategies (defined as foregoing mating chances for first year after offspring's birth). The model examined trade-offs of "father effect" (increased infant survivorship as a result of father's presence, cf. Harpending and Draper 1986) against mating opportunities, across different values of paternity confidence. Whether or not female fertile cycles were seasonally constrained was critical to whether philanderer males would stop roving and settle down. In non-seasonal conditions, there were too many mating opportunities for dominant males to forego, even when infants they had sired were likely to die owing to desertion.

Some degree of seasonality would also be essential for female hominins to maximize their capacity for ovarian cycle synchrony. Where females do synchronize ovulation tightly, there are no benefits to a male in moving from one female to another during the same ovarian cycle and hence for the whole period that both females are cycling together. Females may obtain the same effect by concealment/unpredictability of ovulation. In modeling the optimal day for male desertion of one cycling partner for another, Dunbar (1988: 160) demonstrates that where a male receives no good information about the imminence or occurrence of ovulation, his chances of making the right decision are reduced.

MENSTRUATION GIVES AWAY VITAL INFORMATION TO MALES

In langur monkey populations where seasonality promotes synchrony and undermines male monopoly, females show no clear sign of menstruation or ovulation. We assume for phylogenetic reasons that menstruation has been visible in *Homo.* Even if ovulation is not perfectly predictable in relation to menstruation, this information would allow dominant or philanderer males to mate-guard recently menstrual females until they were pregnant. In other words, menstruation allows males to track female fertility, and favors male monopoly—unlike reproductive synchrony in the absence of menstrual cues. Individual females could use menstrual signals strategically to advertise their imminent fertility, attracting and concentrating paternity on particular males.

The major behavioral ecological study of men, women, and menstruation in a natural fertility population has been Beverly Strassmann's work on the Dogon (1992, 1996, 1997; Strassmann et al. 2012). Dogon cosmology is noted for a severe negative view of menstruation, with women consigned to menstrual huts at this time. Yet, actually, a husband would spend his time talking with his wife in the evenings from outside the menstrual hut; failure to do so would show he did not love her (Calame-Griaule 1965: 242–243). In Dogon belief, a woman is most likely to conceive in the first sex act following menses (cf. Marlowe 2004 on the Hadza). Hence, the husband's attentiveness. Approaching from a Darwinian rather than cultural perspective, Strassmann (1992) proposed that Dogon menstrual taboos function as an anti-cuckoldry device, enabling husbands to keep track of a wife's reproductive condition. She verified that women who visited huts were reliable in indicating their menstrual state (Strassmann 1996). Recently, Strassmann and colleagues (2012) have used genetic data to show that practice of Dogon traditional religion and menstrual observances reduces cuckoldry compared to levels among Christian and Islamic Dogon converts. Muslim husbands were also notified by wives of menstruation, and suffered lower cuckoldry than Christians whose wives were not obliged to notify husbands. What is uncertain is why it should be in the traditional Dogon husband's interest to have his wife signal her imminent fertility so visibly, since the huts are central and public. Strassmann (1992) argues that since men are polygynous, they might not be able to monitor menstruation in each of their wives. But what the menstrual hut visits do enable is monitoring by other men of the patrilineage. Key resources in Dogon economy are millet fields held by patrilineages. So, men of the village patrilineage have a serious concern in legitimacy of father-son inheritance and therefore surveillance of patrilineage wives' cycles. Sanctions of expulsion from the patrilineage and land loss strongly deter within-patrilineage cuckoldry (Strassmann et al. 2012).

An historic example of extreme control over women's fertility through tracking of menstrual state comes from Imperial China. The harems of T'ang dynasty emperors could number in the hundreds. These were organized by a "secretariat of elderly ladies"—the nü-shih—who kept careful records of the date of menstruation, the day and hour of successful sexual unions, and first signs of pregnancy (Potts and Short 1999: 231; van Gulik 1974: 17–18). Concubines and court ladies used a cosmetic device of dots on the cheek to indicate to the emperor that they were menstruating, which later became a standard cosmetic feature (Huo 2004).

Clearly in these cases of societies with significant resource defense polygyny, signaling, practice, and beliefs around menstruation has or had considerable effect on male fitness. In nomadic forager economies more closely resembling evolutionary conditions, signaling associated with menstruation is predicted to arise as a female strategy advertising imminent fertility; in these conditions, men are far less likely to be able to establish control over or coerce women's signaling. Arnhem Land Aboriginals maintained a menstrual cosmology just as elaborate as the Dogon's, with strict prohibitions and taboos applying to women at menses. The *Love Songs of Arnhem Land* recurrently celebrate the failure of the gerontocracy to monitor women's movements at menstruation, singing of lovers' illicit assignations "among the cabbage palm foliage" during their periods of supposedly strict seclusion (Berndt 1978: 61). A Ju/'hoan mother who had started to menstruate again smeared her inner thighs with fat and painted soot around her eyes, or cut a tonsure into the hair of her youngest child to paint it (Wilhelm 1954: 118). A Ju/'hoan girl dressed her finest kaross with red ochre as a sign to men that she was menstruating (Thomas 1959: 234). In these cultural contexts, individual women and girls were choosing to signal their imminent fertility; even where there were strict taboos on contact between menstrual blood, hunters, and their weapons, men were clearly gathering information about female reproductive status.

Among Hadza hunter-gatherers, who are not in general polygynous, most men consider the time right after menstruation the best to get females pregnant (Marlowe 2004), a belief almost surely arising from the need to track menstruation in mates and guard them at that time. A similar belief is found among forest hunter-gatherers such as the Mbendjele (Lewis 2002) and the Mbuti (Turnbull 1984).

In the above examples, from human mating systems ranging between more-or-less monogamous to extremely polygynous, menstruation demonstrably influences male behavior. The extensive ethnographic literature documenting ritual, taboos, and observances around menses substantiates the view that women readily advertise their condition and men are very interested in that information. Elaborate menarcheal ritual of highly standardized form is one of the most invariant features of Khoisan societies (Power and Watts 1997, 1999).

SEASONALITY AND SIGNS OF MENSTRUATION IN *HOMO* LINEAGES

How could the interplay of visible menstruation and greater or lesser seasonality of female reproduction have altered strategies in early humans? Genus *Homo* evolved into a fully terrestrial biped form with larger body size from the Early Pleistocene just as climate started to oscillate with increasing amplitude (Potts 1998). From its African origins *Homo* evolved to exploit increasingly seasonal environments with particularly marked wet/dry season variation (Foley 1993; Reed and Fish 2005). Data on soil chemistry, pollen, and faunal remains indicate increasing aridity and seasonality in tropical Africa from 2.5–1.7 ma (Behrensmeyer et al. 1997; Cerling et al.1988; Reed 1997; Spencer 1997; Vrba et al. 1995). Early *Homo* probably experienced difficulty in getting fats and carbohydrates during dry-season periods of resource stress (Speth 1987, 1989; Speth and Spielman 1983). Scarcity of specific nutrients, resulting in periodic weight loss, would trigger energetic challenge mechanisms for females, leading to some degree of seasonality in reproduction with reduced conception rates following very dry periods.

Early African *Homo erectus* females could have met reproductive costs of larger-brained, more dependent offspring through the combination of increased body size—allowing a greater foraging range—grandmother allocare, and occasional rather than reliable help from mates. Females with helping female kin would be more likely to attract extra help from mates, since they should return to cycling more quickly, having shorter interbirth intervals. Increased fertility rates would feed back into more male mating effort—the extra nutrition would aid quicker conception, and survival of weanlings. Some degree of seasonality combined with polyandrous mating would encourage multimale involvement, preventing single male monopoly, especially in colder, drier climate phases. However, the visibility of menstruation would continue to reward philanderers/dominant males who tracked and guarded menstrual females.

There is no evidence for further increase in cranial capacities among African *Homo erectus* (Anton 2003: Table 2; Potts et al. 2004). From around the beginning of the Middle Pleistocene (780–130 ka), renewed increase marks the speciation of *Homo heidelbergensis* (Rightmire 2001: Figure 4). The few African fossils from 800–600 ka have cranial capacities in the range of 1200–1300cc. While some of this increase can probably be attributed to larger body size (Churchill et al. 2012; Rightmire 1996), it is considered to mark an episode of encephalization (Rightmire 2004, 2009). However, the steepest increase in cranial capacities occurs considerably later—after ~300 ka (e.g., de Miguel and Henneberg 2001: Figure 1; Lee and Wolpoff 2003: Figure 2). African fossils suggest that this last phase was abrupt and coincident with our speciation (Table 1).

From the beginning of the Middle Pleistocene, these increases of cranial capacity placed females under greater pressure to recruit male support through more productive hunting. But visible menstruation would have posed a problem. By cueing males who targeted fertile females, menstruation would enable some males to dominate fertile matings. This could undermine the development of male cooperative hunting strategies, since mate-guarding would be critical in sexual competition for fertile females. Males would have been reluctant to depart on hunts if reproductive success depended on mate-guarding.

Menstruation would have triggered competition not only among males, but also among females, since those who were not cycling, but pregnant or lactating, stood to lose male investment. In any natural fertility population, females who are pregnant, lactating, or post-reproductive outnumber those who are currently cycling. Given very high reproductive costs for females, non-cycling females would share strong interests in working together as coalitions (Key 1998, 2000). In evolutionary contexts of female allocare, coalition members would likely include kin relatives. Indeed, the cycling females who threatened to divert male attention would likely be kin relatives of non-cycling females. Non-cycling females would have two possible responses to this dilemma. They might try to hide the menstruant's condition so that males would not know. But since the signal has potential economic value of attracting male attention, rather than hide it, females are predicted to do the opposite—flaunt it (Knight et al. 1995; Power 1999, 2009; Power and Aiello 1997). Whenever a coalition member menstruated, the whole coalition joined in advertising and amplifying the signal to attract outsider males and their labor to the coalition. We expect females within coalitions to begin to use blood-coloured substances as cosmetics to augment their signals.

This Female Cosmetic Coalitions (FCC) strategy should succeed as long as philanderers were prevented from gaining access to menstrual females and if the extra male attention and mating effort generated were distributed among the whole coalition, benefiting both non-cycling and cycling females. The strategy is well designed for demonstrating commitment to an alliance. Within any coalition, there would be little chance to cheat since each female must clearly show that she foregoes any benefits of trading with philanderer males when cycling before she stands to gain benefits when she is pregnant and lactating. All fertile females alternate between states of cycling and non-cycling. By cooperating in the strategy, a cycling female shows a costly signal of commitment to other females in the alliance (cf. Alcorta and Sosis 2005; Gintis et al. 2001; Irons 2001; Power 2009; Zahavi and Zahavi 1997).

Between female coalitions, a competitive dynamic would be expected as they strove to attract available male labor. This should drive an evolutionary arms race of increasingly elaborate cosmetic advertising, resulting in ritualistic amplification of displays. This could involve use of mineral pigment such as red ochre to amplify and broadcast the cosmetic menstrual signal, with multimedia effects of movement, song, and dance.

The FCC model offers a prototype 'moral' strategy, with non-cycling females aiming to obstruct and control sexual access to cycling females—a basis for the emergence

TABLE 1. MIDDLE PLEISTOCENE AND EARLIER LATE PLEISTOCENE CRANIAL CAPACITIES IN AFRICA AND WESTERN EURASIA.

Sample	Fossil	Date Estimate (ka)	Cranial Volume (cm³)	Sources for Revisions and Additions
African pre-*Homo sapiens*	Ternifine (1)	750	1300?	
	Saldanha	700	1217	Klein et al. 2007
	Bodo	600	1275	
	Sale	400	930	
	Ndutu	400	1100	Bräuer 2008
	Ileret	270	1400	
	Florisbad	260	1280	
	Kabwe	250?	1320	Stringer 2011
	Ngaloba	250	1284	Manega 1993: 123
	Eliye Springs	200	1210	Bräuer et al. 2004
	Eyasi 1	200	1235	Trinkaus 2004
	sample mean		**1232**	
	s.d.		**125**	
African Middle Pleistocene *Homo sapiens*	Omo 1	195	1400	McDougal et al. 2005
	Omo 2 (2)	195	1430	McDougal et al. 2005
	Jebel Irhoud 1	160	1426	
	Jebel Irhoud 2	160	1378	
	Herto	160	1450	White et al. 2003
	Singa	150	1550	
	Border Cave 1 (3)	150	1478	Grün and Beaumont 2001
	sample mean		**1445**	
	s.d.		**57**	
Levantine Early Late Pleistocene *Homo sapiens*	Skhul 1	115	1450	Wood 2011
	Skhul 2	115	1300	
	Skhul 4	100	1555	
	Skhul 5	115	1499	
	Skhul 9	110	1587	
	Qafzeh 6	90	1561	
	Qafzeh 9	90	1531	
	Qafzeh 11	90	1280	
	sample mean		**1470**	
	s.d.		**119**	

of the puberty rituals, taboos, and prohibitions that surround menstruation in so many ethnographic accounts (Knight 1991). It also yields a prototype symbolic strategy, with collective agreement that fake 'blood' stands for real blood, hence fertility. Yet the strategy emerges through purely Darwinian dynamics, ultimately driven by male sexual selection of female ritual participants.

On the face of it, it sounds improbable that males would choose cosmetic menstruation. Why would male observers sexually select cosmetically decorated females? On a basis of honest signaling, why would males be interested in fake menstruation?

The choosy males would be investors who have every interest in keeping philanderers at bay. Consider the model as a game of alternative strategies—Female A uses cosmetics as part of her ritual coalition whenever one of them menstruates; Female B and all her female neighbors use no cosmetics. Male A is prepared to work/invest to gain access; Male B tries a philanderer strategy, moving to the next cycling fertile female, neglecting the previous partner once she is pregnant. Very quickly, Male A will end up working/doing bride-service for Female A's coalition, since he has no competition from Male B. Male A gains regular fitness (RS) as a result. Male B will pair up with Female B, but is then liable to abandon her if he finds a new cycling female. She then has little support during pregnancy/breastfeeding. The question will be whether Male B gains sufficient fitness via a roving strategy of picking up cycling, non-cosmetic females. If Male A is not able to compete with Male B in terms of dominance, he is better off choosing the cosmetic females. Because Female B and her non-cosmetic female neighbors get the attentions, but no reliable investment, from Male B, they discourage any investment from the likes of Male A. Once costs of encephalization begin to bite and cooperative strategies are needed to support offspring, how many females will be choosing philanderers in preference to investors? Those females are not likely to be ancestors of large-brained hominins like ourselves or Neanderthals. We predict that the philanderer male's supply of non-cosmetic females will dry up quickly.

The ritual cosmetic strategy can be considered as costly signaling of quality by female coalition members (Power 2009). Few males would be likely to be deceived about which females were actually pregnant/lactating and which

TABLE 1. (continued).

Sample	Fossil	Date Estimate (ka)	Cranial Volume (cm^3)	Sources for Revisions and Additions
Eurasian Middle Pleistocene >200 ka	Atapuerca 4	400	1390	Stringer 2012 (4)
	Atapuerca 5	400	1125	Stringer 2012 (4)
	Atapuerca 6	400	1153	Stringer 2012 (4)
	Ceprano	400	1185	Manzi et al. 2010
	Arago	400	1139	
	Swanscombe	400	1305	
	Petralona	300	1266	
	Reiingen	300	1432	
	Steinheim1	300	1140	
	Ehringsdorf	203	1450	
	sample mean		**1259**	
	s.d.		**129**	
Eurasian MIS 6 and MIS 5	Vertesszollos2	186	1335	
	Biache	178	1200	
	Krapina D	130	1450	
	Krapina C	130	1200	
	Apidima 2	130	1454	Harvati et al. 2011b
	Saccopastore 1	120	1234	
	Saccopastore 2	120	1295	
	Tabun C	120	1270	
	Ganovce	120	1320	Kneblova 1958
	sample mean		**1306**	
	s.d.		**95**	

Values are adapted from de Miguel and Henneburg (2001). Notes:

1) Ternifine cc estimate based only on a parietal, Wolpoff 1996–97.
2) Omo 2 is included as *H. sapiens* on dating grounds and growing appreciation of the potential morphological variation among early *H. sapiens* (cf. Harvati et al. 2011a).
3) Border Cave 1 is treated as Middle Pleistocene as a 5BS derivation is just as plausible as 4BS at ~82 ka (Grün and Beaumont 2001: 478).
4) A periodization of Sima de los Huesos between ~350–400 ka on genetic and morphological grounds (Stringer 2012) is favored here over current radiometric estimates of ~600 ka (>530 ka) (Bischoff et al. 2007).

really menstrual. In the first place, the strategy works to deter would-be philanderer males from targeting menstrual females, and demonstrates the solidarity of the female coalition (with male relatives in support). What is the honest signal and what is the quality choosy males would be interested in assessing? Suppose a young female starts to menstruate, prompting her kin to stage a ritual. The performance advertizes a female of maximum reproductive value and also demonstrates, in ways that are hard-to-fake and easy-to-judge, the extent of the female's kin support network. The pubertal female whose kin coalition stages body-paint display is signaling to discriminating males: "Invest in me because I have extensive kin support and my babies will also have it!" She also demonstrates her 'moral' quality, showing non-investor males are not welcome.

Power and Watts (1996) proposed two stages of this ritualization process, determined fundamentally by degree of reproductive stress on females. The initial situation, during the early phase of brain expansion in *H. heidelbergensis*, would produce context-dependent, ad hoc ritualized displays triggered by incidence of menstruation in the local population. Female coalitions would have used the strategy opportunistically to attract and retain male support, deterring any male philanderers' attempts to monopolize menstruating females. This implies little planning depth in obtaining cosmetic materials, with considerable reliance on biodegradable matter. We predict only sporadic use of red ochre during this phase.

As cranial capacities increased again in the period culminating in modern human speciation, we expect female coalitions with male kin support to have used the cosmetic strategy habitually to motivate outsider male labor and investment whether or not any females were actually menstrual. Greater regularity, planning, and organization of performances would produce abundant and regular use of ochre where regionally available. We also predict that where good quality ochre was not locally available, procurement distances should exceed or equal those documented for exotic lithic raw materials. Raising previously ad hoc ritualized display to regular ritual performance would institutionalize an economic division of labor and elaborate forms of social cooperation both between the sexes and between kin groups. It should also permit relaxation of selection pressures for robusticity (cf. Churchill et al. 2012), especially in females, with reduction of stress experienced by juveniles. It should furthermore promote investment in campsites with females and offspring able to stay home while male hunters depart on logistic hunts. As soon as male mates respond to ritualized signaling by going hunting to get access to female coalition members—effectively performing bride-service—they would be actively investing in that female coalition (and their own offspring). Male choice of ritually, cosmetically decorated females should drive the explosive spread of these ritual traditions. We therefore predict these forces of sexual selection were implicated in the speciation of modern humans c. 200 ka in Africa.

THE FEMALE COSMETIC COALITIONS MODEL: CURRENT EVIDENCE

The FCC model produces a range of predictions testable against data in the archaeological, fossil, and ethnographic records (see Power 2009: Table 14.2). The two main falsifiable hypotheses are: i) the earliest evidence of symbolic behavior will be found in a cosmetics industry focused on red pigment; and, ii) the emergence of the strategy should correlate with increase in brain volume as an index of female reproductive stress. More precisely, initial red pigment usage could occur as early as ~800 ka; it should certainly be evident from about 300 ka onwards, with ubiquitous regular use in Africa predicted by the time of our speciation—between ~200–150 ka. The shift from irregular or localized regular use, to ubiquitous regular use should appear quite abruptly between ~250 ka to ~150 ka.

An earlier version of these predictions was published over fifteen years ago (Knight et al. 1995; Power and Aiello 1997; Power and Watts 1996). The spate of subsequent publications illuminating the African Middle Stone Age (MSA) and Near Eastern pigment record (Barham 2002; Dayet et al. 2013; d'Errico et al. 2010; Henshilwood et al. 2001, 2002, 2009; Hodgskiss 2012; Hovers et al. 2003; Marean et al. 2007; McBrearty and Brooks 2000: 528; Salomon et al. 2012; van Peer et al. 2004; Watts 1999, 2002, 2009, 2010) have largely borne them out.

Setting aside issues of artifactual status (e.g., Butzer 1980; Wreschner 1985), how confident can we be that archaeological materials producing a colored streak when abraded were used as pigments? It has repeatedly been objected that other explanations are plausible—ochre may have served as medicine, insect repellent, odor suppressant, sun-block, insulation against the cold, tanning agent, or as a functional ingredient in hafting mastics (e.g., Bahn and Vertut 1988; Klein 1995; Lombard 2007; Wadley 1993; Wadley et al. 2004). Archaeological and experimental support for ochre sometimes having a functional role in hafting cements is fairly compelling (Lombard 2007; Wadley et al. 2009), while recent experimental work has established the efficacy of red ochre in producing pliable hides resistant to desiccation and putrefaction (Rifkin 2011). Here we confine ourselves to four observations. First, none of the proposed banausic uses of ochre carry any strong implications for color selection,[1] but where large, ochre assemblages have been studied in detail, preferential use of the reddest and most saturated materials has been reported (Hodgskiss 2012; Watts 2009, 2010; see also Salomon et al. 2012 for complementary findings). Second, archaeological support for any of the banausic explanations (e.g., Lombard 2007) postdates symbolic culture, which in Africa and the Levant extends back at least 100,000 years (d'Errico and Stringer 2011 with refs.; Henshilwood et al. 2011). Third, banausic hypotheses would only predict the use of locally available materials, and to our knowledge have never been invoked in relation to glittery specularite. While little work has been done on sourcing early 'pigment' occurrences, with the establishment of symbolic culture there are indications of relatively long-distance procurement (e.g., Salomon et al. 2012; see also Watts 1999: 119; 2009: 83–86). Finally, we note that the hide-working experiments involved large quantities of ochre—requiring hours of grinding, inconsistent with the quantities of pigment generally recovered and with the small size of many archaeological utilized pieces (Rifkin 2012; see also Watts 2009: 90). Our point is simply that, singly or collectively, it seems highly unlikely that such uses could provide an adequate general account for the phenomenon.

We argue it is most parsimonious to assume that, at least in early contexts, ochre was primarily a pigment and served as a cosmetic bodypaint, possibly also decorating hides and other organic materials. Both from a Darwinian signal evolution perspective and from a social anthropological perspective, it is reasonable to infer that the principal domain of use would have been ritual display (Power 2009; Watts 2009).

A brief review of claims for Early Pleistocene pigment use (Watts 2010: Supplementary online material, 10–11) concluded that on available evidence there is no good reason to accept a designation as pigment. The FCC model predicts earliest pigment use could occur from the period of *H. heidelbergensis* encephalization, albeit sporadically. There are a few claims for early occurrences that may fall into the earlier Middle Pleistocene, but the contexts are generally poorly dated and/or the claims inadequately supported. In Europe, at Isernia La Pineta (Italy), pebbles and fragments of ochreous material were identified (Cremaschi and Peretto 1988) in a context dated to ~610 ka (Coltorti et al. 2005). Beaumont has claimed Acheulean pigment use at three sites in the Northern Cape (South Africa) (Beaumont and Vogel 2006: 222). On the basis of recent dating estimates of ~500 ka (Porat et al. 2010) for the succeeding Fauresmith industry in the region—transitional between the Acheulean and Middle Stone Age—these contexts are older (the Wonderwerk claim extends to deposits ~1 ma). Unfortunately, no substantiating details are provided, and in the case of the two Kathu sites, the cited support (Beaumont 1990a) does not mention pigment in the relevant contexts. Assemblages from all three sites are currently being re-investigated. Hunsgi Locality 5 (an Early Acheulean site in southern India) certainly looks like pigment use, with a collection of introduced 'haematite' pebbles including a ground piece, but the only age estimate is a minimum one of ~300 ka (Szabo et al. 1990, cf. Mishra 1992 for evaluation), while the Early Acheulean in the region extends back at least 1.07 ma (Pappu et al. 2011).

Pigments are definitely present in the Fauresmith horizon of Kathu Pan 1 in the Northern Cape (Beaumont 1990a; Wilkins and Chazan 2012), associated with dating estimates of ~500 ka (Porat et al. 2010). These include scraped specularite and probably ground red ochre (I.W., pers. obs., work in progress). Currently, this is the world's earliest reasonably secure pigment occurrence. Dating estimates for the early MSA in the region (Grün et al. 1996; Porat et al. 2010) suggest that the Fauresmith lasted until at least ~300 ka. Beaumont has reported specularite and/or red ochre from other Fauresmith contexts in the region (Beaumont 1990b; 2004) and one of us (I.W., work in progress) has confirmed the utilization of both materials in Fauresmith horizons at Wonderwerk Cave. The location of these pigments 140m from the cave entrance does not fit well with any banausic interpretation, but could fit some form of firelit display. It seems, therefore, that in a region where eye-catching specularite outcrops are quite widespread (Beaumont 1973), a localized tradition of pigment use predates ~300 ka.

Pigments associated with the early MSA industries between ~300–200 ka are more widely distributed (McBrearty and Brooks 2000: 528; Barham 2002; van Peer et al. 2004; see also Watts 2009: Table 4.2). Focusing on rock shelter sequences—the sites most likely to have been campsites —and on South Africa, as the most intensively studied region, pigments are ubiquitous in the Late Pleistocene MSA (Watts 1999), but are typically absent in the earliest MSA aggregates (Mason 1957: 135 [Cave of Hearths]; Volman 1981: 325 [Peers Cave]; Watts 1998: 569, and Figure 7.24 [Bushman Rock Shelter]). Border Cave is one of the few sequences with dated Middle Pleistocene deposits; pigment is very rare in the basal aggregate (>227 ka), becoming a regular feature within MIS 6 (Watts 2009: Figure 4.1). A similar shift was identified at Bushman Rock Shelter (Watts 1998: Figure 7.24), in levels tentatively dated to MIS 6 on geomorphological grounds (Volman 1981: 96 citing Butzer and Vogel 1979). Regular use of red ochre is documented at Pinnacle Point from initial occupation at ~164 ka (Watts 2010). This implies that the earlier cluster of Northern Cape Fauresmith occurrences, with continuity to the early MSA indicated at Wonderwerk and Kathu Pan, was a localized phenomenon. Current evidence suggests ubiquity and regularity of use were not established until within MIS 6, possibly an abrupt shift. This may correlate with the final phase of encephalization, which itself seems quite abrupt (see Table 1). This would be congruent with one of the key predictions of the FCC model.

Considering the pigment record as the remains of ritual bodypainting traditions, Watts (1998, 1999) argued that the MSA color selection criteria compared closely to those of historic Khoisan populations (see also Watts 2010: Supplementary Material online, 7–10). The Khoisan social context most persistently involving pigment use is a girl's menarcheal ritual (Knight et al. 1995). The FCC hypothesis currently stands as the only Darwinian explanation of why red ochre became the cultural species marker of *Homo sapiens* as we emerged in Africa and migrated throughout the Old World.

Shell beads, some ochre-stained (Bouzouggar et al. 2007; d'Errico et al. 2005; Vanhaeren et al. 2006) and geometric engravings on ochre (d'Errico et al. 2012; Henshilwood et al. 2002, 2009; Mackay and Welz 2008; Watts 2010) testify to symbolic culture in Africa prior to or at around the time of initial *Homo sapiens* migrations beyond the continent. The geometric engraving tradition currently extends back to ~100 ka (Henshilwood et al. 2009), while the beads mainly lie between 80–73 ka. In the same time range is the ritual elaboration of two early *H sapiens* burials in the Levant (McCown 1937; Vandermeersch 1970). The claim that earlier African evidence for the regular and ubiquitous use of red ochre represents the earliest symbolic tradition now appears more plausible than it did twenty years ago.

WHAT ABOUT THE NEANDERTHALS?

A number of recent finds support the view of a multispecies or multipopulation emergence of symbolic culture (d'Errico 2003; Zilhão 2006). Neanderthal symbolic behaviors are attested by pigments associated with marine shells from ~45–50ka in Murcia, S.E. Spain (Zilhao et al. 2010), as well as evidence for ornamental use of raptor feathers from similar or earlier dates (Morin and Laroulandie 2012; Peresani et al. 2010). Because the FCC strategy is driven by female reproductive stress associated with encephalization, we expect both lineages, our own ancestors in Africa and those of the Neanderthals in Eurasia, to adopt it. Yet the Eurasian and African records of pigment use differ significantly over the past 200,000 years (Watts 2009). As noted by Wreschner (1985: 389), there is a find-gap in Europe of approximately 100,000 years, between ~200 ka and ~100 ka, precisely the period when, in Africa, it seems that red ochre use shifted from being either irregular, or regular but localized, to becoming ubiquitous and regular. Watts (2009) proposes that this is the most significant difference between the archaeological records of the two lineages for this period. How can the FCC model account for this?

NEANDERTHAL ENERGETICS AND SEASONALITY

Before investigating possible reasons for this difference, we should confirm that Neanderthal females would have had similar reproductive costs to modern female African ancestors. These costs can be compared in terms of absolute metabolic costs of brain and overall body maintenance. Any difference in rate of maturation of offspring would also affect the rate at which energy must be provided by the mother.

Overall, if we compare mean cranial capacity through time for Eurasian and African lineages, there are no real differences in expansion rates of brain size (Figure 2, see Table 1).

There is one exception: in the period from c. 200–100 ka, Neanderthal mean cranial capacity (1,306 cc) falls below the African mean (1,445 cc). Otherwise, Neanderthal cranial capacities maintain parity with those of African lineage. This implies Neanderthals had a late burst of encephalization after c. 100 ka, taking them to a mean over 1,500 cc between 70 and 40 ka.

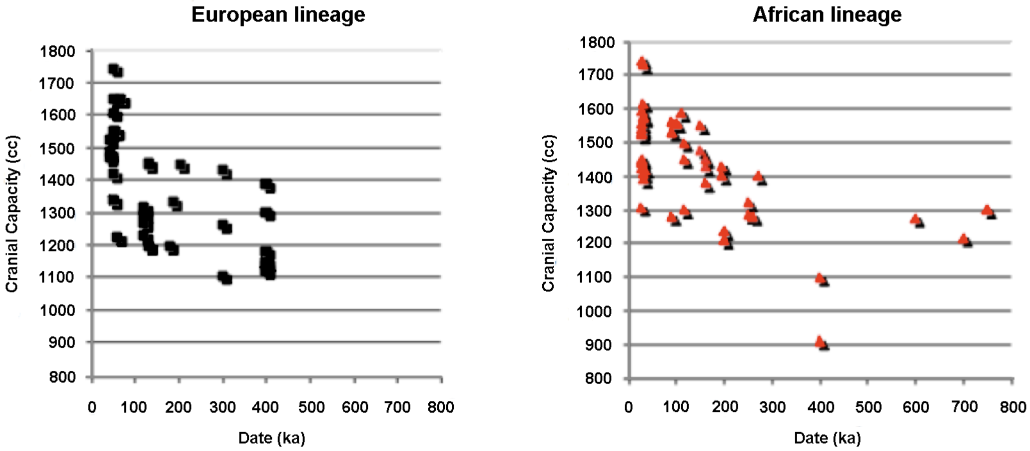

Figure 2. European vs. African cranial capacity through time for descendants of H. heidelbergensis. *Note: Data are based on cranial capacities averaged for individual specimens from all estimates listed by De Miguel and Henneberg (2001), down to 25 ka. Specimens added to their list include: Herto (Africa, 160 ka) and Apidima (Europe, 130 ka); Zuttiyeh (Galilee) has been removed, and juveniles are omitted. Dates have been adjusted for the following: Saldanha (700 ka); Ceprano (400 ka); Ndutu (400 ka); Swanscombe (400 ka); Atapuerca 4, 5, and 6 (400 ka); Florisbad (260 ka); Kabwe (250 ka); Ngaloba (250 ka); Eliye Springs (200 ka); Eyasi (200 ka); Omo 1 (195 ka); Omo 2 (195 ka); Jebel Irhoud 1 and 2 (160 ka); Saccopastore 1 and 2 (120 ka); Tabun C (120 ka); Ganovce (120 ka); Skhul 1, 2, and 5 (115 ka); Skhul 4 (100 ka); Skhul 9 (110 ka); Qafzeh 6, 9, and 11 (90 ka); Border Cave (150 ka); Fontéchevade (50 ka); Spy (40 ka); Mladec 1, 2, and 5 (31 ka).*

Neanderthals were born with similar brain volumes to moderns, and growth rates appear to be at the upper end of early modern human variation (Ponce de Leon et al. 2008). Recent analysis of a Middle Paleolithic sample of Neanderthal and modern human juveniles supports significantly faster dental maturation rates in Neanderthals, with early modern humans more similar to recent humans (Smith et al. 2010). This indicates subtle developmental difference, and implies that Neanderthal mothers would have been under increased energetic pressure in raising large-brained offspring at a faster growth rate.

In addition, reproductive energetics between our ancestors and Neanderthals may have differed owing to body mass and shape. Neanderthals tended towards relatively large bodyweights (Hartwig-Scherer 1994; Ruff, Trinkaus and Holliday 1997), while emerging moderns became more gracile, losing robusticity (Churchill et al. 2012; Kappelman 1996; Ruff, Trinkaus and Holliday 1997). Neanderthals appear adapted to shifting cool temperate to periglacial conditions, showing stocky body form (Trinkaus 1989) and foreshortened limbs (Holliday 1997) with exceptional trunk width (Ruff 1994). Large noses and the robusticity indicating high activity levels may be cold adaptations (Churchill 1998, 2006; but see Rae et al. 2006). However, Neanderthals survived over a vast climatically differentiated area through climatically unstable times (Finlayson 2004; Schwartz et al. 1999).

Sorenson and Leonard (2001) model conservative estimates of total energy expenditure (TEE kcal/day) for Neanderthals from basal metabolic rate (BMR) estimates elevated as a cold adaptation, assuming heavy physical activity levels. With a range of 3,000–5,000 kcal/day for females, and 4,000–6,000 kcal/day for males, Neanderthals were at the higher end or exceeding the estimates for contemporary foraging populations, including the high energy requirements of Igloolik Inuit. In updated modeling, Snodgrass and Leonard (2009) apply fat-free mass standards to facilitate comparisons between populations with diverse body sizes and composition. Drawing on Siberian analogs, they produce TEE estimates for summer vs. winter and low vs. high activity levels for female and male Neanderthals. They suggest females in particular would have almost doubled their energy budgets between low summer and high winter activity levels, factoring in acute cold stress and high protein diets.

Using Tierra del Fuego groups as an analog, Steegmann et al. (2002) propose a set of Neanderthal cold adaptations, including thermogenic brown adipose tissue. This carries high metabolic costs, again producing high (3,300–4,500 kcal/day) estimates for winter foraging. Deriving BMR estimates from surface area, and using a half-size reconstruction of a Neanderthal male to verify the latter, Churchill (2006) arrives at a similar result of 3,500–5,000 kcal/day in cold conditions. Weaver and Steudel-Numbers (2005: Table 3) focus on the effects of limb length on costs of locomotion, estimating that with their shorter limbs and greater body mass, Neanderthals had foraging costs around 200 kcal/day greater than Upper Paleolithic moderns.

This suggests a 10% greater energetic requirement for Neanderthals compared with modern human ancestors (Macdonald et al. 2009). Adopting a comparative behavioral ecological approach, focusing on difference in foraging, mobility, seasonal flexibility, and energetics, Roebroeks and Verpoorte (2009) argue that the higher energy requirements of Neanderthals relative to moderns may explain differences in the archaeological record in use of space, investment in campsites, length of stays, and frequency of moves. Social organization could likewise have differed between Middle Paleolithic Neanderthals and Upper Paleolithic modern humans (MacDonald and Roebroeks 2005: 966–967). Energy cost differences between populations and between the sexes in each population probably altered the costs and benefits of cooperation between males and females (Key and Aiello 1999, 2000).

Do the raised energy costs of female Neanderthals imply they should have developed symbolic strategies first? We need to consider the implications for reproduction of this very high energetic expenditure in highly seasonal environments. Reproductive seasonality will result if there is a significant energy deficit for mothers in any part of the year. If demands of Neanderthal thermoregulation would have been greatest when calories were hardest to obtain, it is probable that Neanderthals had more seasonal reproduction than any other hominin ever (see also Mussi 2007; Snodgrass and Leonard 2009). A critical factor in seasonal availability of resources and female energy balance would have been the fat-protein ratio (Cachel 1997; Speth 1991). Modern humans are limited in the amount of protein they can consume without accompanying fat or carbohydrates; this protein ceiling is lower in pregnant women. One result of an excess protein diet is calciuria, a calcium/phosphorus imbalance, leading to decline in bone mass. For skeletally robust Neanderthals, Cachel (1997) argues, this would be additional physiological stress, and constraint on fertility. During glacial winters, with lack of alternative plant resources especially in higher latitudes, Neanderthals must have relied on terrestrial mammal fat, particularly targeting large-bodied prey; yet these animals themselves would have been very lean from late winter to early spring. Modern human Arctic hunters under traditional foraging conditions show significant conception peaks in early spring to summer (with returning light) (Condon 1991). Mussi (2007) notes that marine mammals can provide Arctic populations with sufficient fats for the winter months, whereas terrestrial mammals only fatten later in summer. Hence, she proposes a late summer conception peak for Neanderthals.

The MIS 6 glacial cycle, lasting from 190–130 ka, was more protracted, with much more extensive ice sheets than MIS 8 (Scott and Ashton 2011). Energetic challenge to ovarian function is the best predictor of birth seasonality in contemporary humans (Ellison 1994: 265–269; Bronson 1995: 147–151). An energetic challenge model suggests that this period could have featured highly seasonal patterns of hominin conception and birth rates, with fine-tuning of ovarian function to metabolic cues. The increase in Neanderthal brain size appears to stall relative to African brain sizes between 200–100 ka, largely coinciding with MIS 6. This strongly suggests Neanderthal females came under severe energetic constraints.

If Neanderthals during glacial cycles had more pronounced seasonal reproduction than African modern counterparts in equatorial zones, this likely had consequences for male and female reproductive strategies. In Power's (2001) model, seasonal reproduction such that a male is unlikely to access more than one female per year, combined with a father effect, strongly undermines a philanderer or roving male strategy. We argue that such conditions prevailed in Europe during the glaciations of the past 300–400,000 years with severe seasonal energetic challenge to both females and offspring.

Strong reproductive seasonality would give females a built in protection against philandering by Neanderthal males, favoring pair-bonding and investor males over those tending to philander. However, what happens when climate switched from cold to warmer, wetter conditions in interglacials or interstadials? Neanderthal females could lose this effect. Less acute cold stress would reduce the disparity of summer and winter energy budgets for females. Warmer and longer growing seasons would produce more sources of carbohydrates and fats from insects, honey, fruit, roots, nuts, eggs, small game, etc. While some large-bodied, fat-bearing prey species would diminish during warmer climate stages, those species replacing them would retain condition through more of the year. Alternative fat sources could also come from marine and riverine environments (Finlayson 2004: 96; Hardy and Moncel 2011).

In those conditions, Neanderthal females would extend the period of fertile cycles through more of the year. This in turn enables male philanderers to seek fertile females in different seasons, accessing more than one female a year, undermining levels of male investment. When conception/birth seasons are extended sufficiently to allow males to switch between females, the FCC model predicts Neanderthal females would resort to cultural cosmetic strategies in coalitions to resist male philanderers. This leads us to posit a Seasonality Thermostat (ST) hypothesis as a refinement to the FCC model, with the following predictions: i) when it is very cold and dry, seasonality constrains Neanderthal males to pair-bond support; and, ii) when it gets warm and wet, to the extent that birth seasonality is relaxed, we expect Neanderthal use of red cosmetics. By contrast in modern ancestry, with less seasonal constraint to reproduction and hence lower pair-bond stability, we predict increasing regularity and reliance on the cosmetic coalition strategy, driven in the end by sexual selection.

The langur monkey example discussed above showed a capacity for flexibility within one species. Physiologically distinct signals develop under different environmental conditions. Populations of Neanderthals and modern humans would have an even greater strategic flexibility afforded by cultural mechanisms, rather than only physiological ones. The monkey model also makes clear why the divergence of strategies within *Homo* populations would become even more marked (Figure 3).

Conditions of strong seasonality do not just imply that Neanderthal females would not be motivated to amplify signals culturally; they would be positively motivated to conceal physiological signals. To the extent that Neanderthal females used seasonality effects to keep males working for them, we predict they should *suppress* visible signs of menstruation. This is because menstruation, by giving would-be philanderers information, undermines the sea-

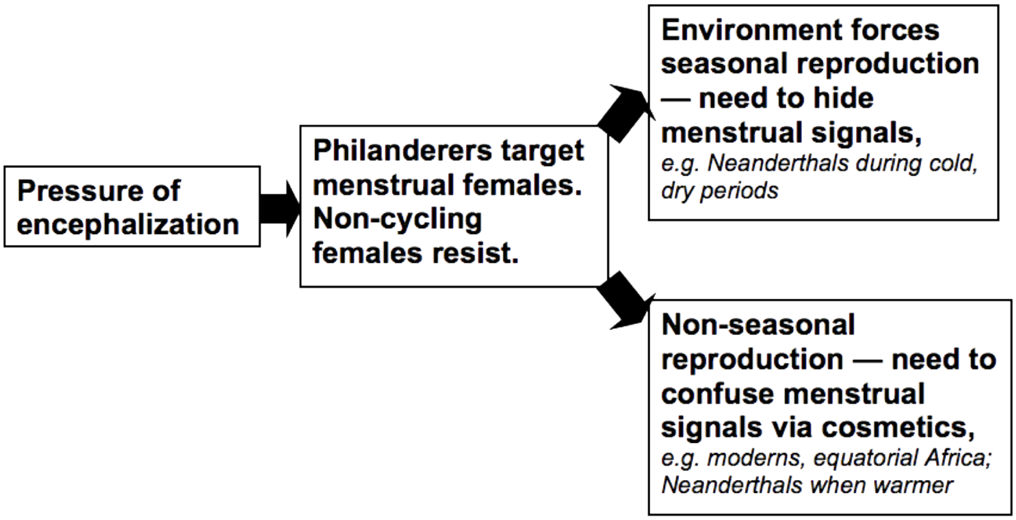

Figure 3. Divergent strategies in descendants of H. heidelbergensis.

sonal effects favoring investor males. Neanderthal females could even have come under selection pressure to reduce visible bleeding, but they could also use cultural means such as clothing (Sorenson 2009) to avoid (extra-pair?) males knowing. So in cold, dry Ice Ages with marked seasonality of reproduction, Neanderthals should hide menstruation where possible, and definitely not amplify their signals. In terms of cultural evolution of pigment use, this would undermine any "ratchet effect" (Tomasello 1999: 5; Tomasello et al. 1993) of accumulating and building on cultural knowledge. If such cultural traditions were recurrently abandoned at the shift into glacial phases (especially MIS 6), this could prevent cosmetic signaling being driven by sexual selection in the way it was for moderns. A further possibility is that the sexual selection effect was delayed until later—potentially in conjunction with late accelerated encephalization after c. 100 ka—and localized in the Neanderthal case.[2]

CORRELATING NEANDERTHAL PIGMENT USE WITH CLIMATE RECORD

Now that the FCC model has been refined with these seasonality thermostat predictions, we can ask how well Neanderthal pigment use fits the predicted pattern (Figure 4a, b). Like the claim for Isernia (above), the next two earliest claims for Eurasian pigment use (de Lumley 1966: 50; Howell 1966: 129) remain poorly substantiated (Butzer 1980; Wreschner 1983, 1985). Should the Terra Amata claim for deliberate abrasion be confirmed by further analysis, it would take pigment use back to either MIS 9.3 (~322–335 ka) or MIS 11.3 (~395–425 ka), both representing peak interglacial conditions (see Falguères et al. 1991 for dating estimates, Valensi 2001 for faunal and palynological references). A more secure claim, but lacking evidence of use-wear, comes from Maastricht-Belvédère, dating to either MIS 9 or MIS 7 (Roebroeks et al. 2012). Two sites (Achenheim and Bečov I) document grinding of red ochre in MIS 7 (Wernert 1957: 211; Marshack 1981), with a further probable red ochre occurrence (Ehringsdorf) from this period (Svoboda et al. 1996: 96, citing Behm-Blancke 1960). A single piece of ground red ochre from Combe Grenal layer 58 (Demars 1992) probably dates to MIS 6 (Delpeche and Prat 1995). Combe Grenal aside, all Middle Pleistocene occurrences are from interglacial contexts. The apparent correlation is unlikely to be a function of demographic changes influencing archaeological visibility, as in northwestern Europe peak population densities are inferred for the cool, open environments of the mammoth-steppe (Scott and Ashton 2011), while in southern Europe, population extinctions or migration during glacial maxima should not be an issue. The seasonality thermostat hypothesis offers a plausible explanation for the well-supported MIS 7 occurrences, and possible earlier interglacial occurrences.

The hypothesis, however, goes on to predict renewed use in MIS 5.5 (128–116 ka), the Last Interglacial *sensu stricto*. This is not currently supported, although archaeological visibility of the interglacial is low across Europe, with only seven shelter occupations (Slimak et al 2010; Wenzel 2007: Figure 12.1). Later in MIS 5 (widely treated in the European context as the beginning of the last glacial cycle, but containing two mild sub-phases, 5.3 and 5.1) there is the striking Tata plaque from Hungary. This polished and red-ochred section of a mammoth molar (Marshack 1976; Vértes 1959) is associated with a dating estimate of ~100 ka (Hausmann and Brunnacker 1988), possibly correlating to MIS 5.3. Claims have been made for pigments in other sites predating MIS 4 (La Micoque, Level 3, Demars 1992:189, citing Bordes 1984, but see San Juan 1990: 232; Les Tares, Wreschner 1983: 90, citing a pers. comm. from J.P. Texier in 1976; el Castillo, Obermaier 1925: 291), but on the scant details available these do not appear compelling. Below we consider the case of Pech de l'Azé IV.

For the Late Pleistocene, despite the large number of sites (>55) where claims for pigments in Neanderthal contexts have been made (for literature surveys touching on most of these sites see Couraud 1991; Demars 1992; Harrold 1989; San Juan 1990; Wreschner 1983), the quality of published information is generally inadequate. Assem-

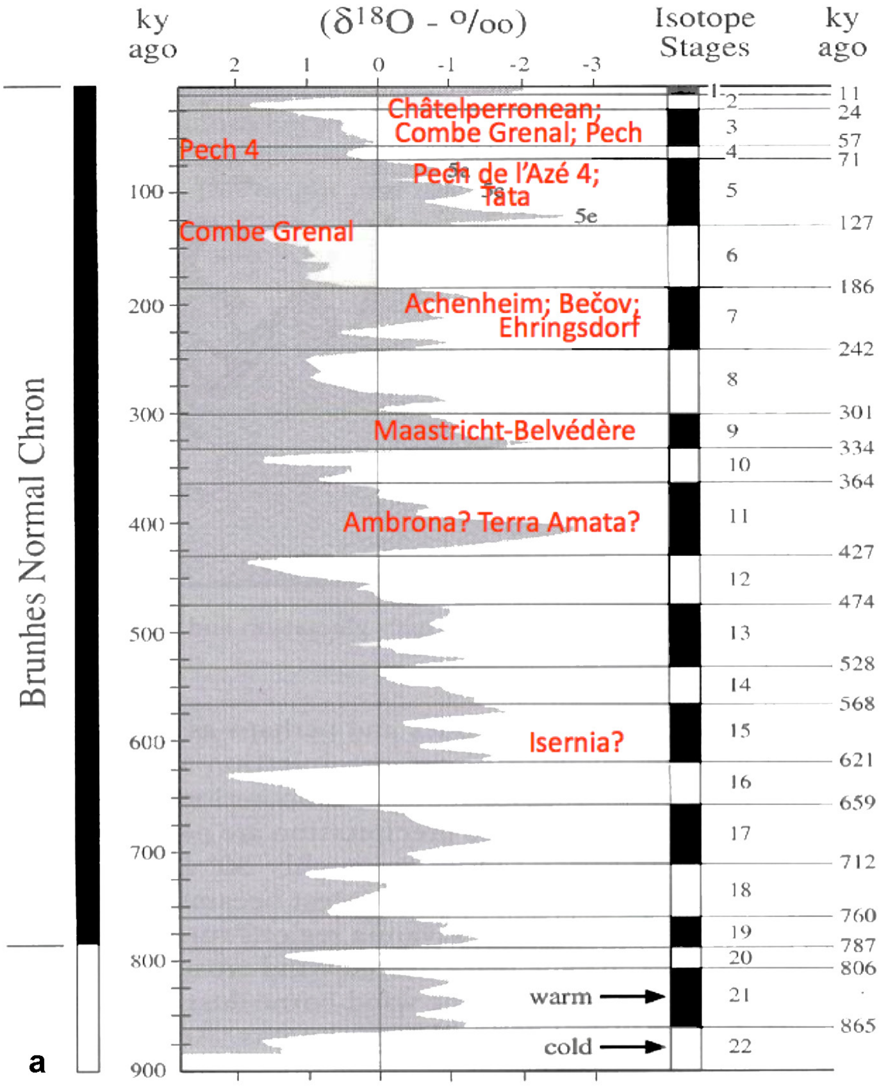

Figure 4. a) European ochre finds during Middle to Late Pleistocene climate cycles.

blage level analyses are available for six sites: Pech I, Arcy-sur-Cure, Caminade Est, Cueva Antón, Cueva de los Aviones, and Cioarei-Borsteni. The triple requirement for deep sequences, adequate information on the pigments, together with paleoenvironmental indices and/or chronometric dating, greatly reduces the pool of potential test-sites.

The long Mousterian sequences of Pech de l'Azé IV and Combe Grenal, with temperate and cold period occupations, provide an opportunity to correlate Late Pleistocene Neanderthal pigment use with paleoclimate at a finer level of resolution. At Pech de l'Azé IV, red pigments might have been expected in basal Layer 8, dated to the mild sub-stage of MIS 5.3 (~100 ka, Dibble et al. 2009). But their earliest appearance is in Bordes' Level J3b (Demars 1992), equivalent to Level 6a of recent excavations (Dibble and McPherron 2006). Faunal proxies and dating estimates (Sandgathe et al. 2011: 221–222) suggest this dates to the final mild sub-stage of MIS 5 (5.1), centered on ~80 ka. In overlying layers (5–4 of the recent excavations, Bordes' J1–I1), with dating estimates from the glacial of MIS 4, manganese predominates, although red ochre is present in Layer I2. The greatest concentration of ochre (in the youngest Mousterian of Acheulean Tradition horizon) is associated with temperate conditions within MIS 3 (Richter et al. 2013; see also Soressi et al. 2008: 109 for the MAT A and MAT B sequence at Pech I).

At Combe Grenal, again using Demars' (1992) pigment inventory, red ochre was encountered in Levels 21, 14, 12, and 7, with pollen indicating short-lived episodes of milder climate within MIS 3 in Levels 22–20, 13–11 and 8 to 7 (Mellars 1996: 40). Intriguingly, black manganese (first encountered in Level 35, with high frequencies in Levels 25–23 and a smaller cluster in Level 17) correlates with extreme cold conditions (Levels 35–23 representing the glacial of MIS 4, pollen from Layer 17 indicating a cold episode early in MIS 3) (Mellars 1996: 39).

Both Combe Grenal and Pech VI sequences suggest that red ochre use largely correlates with milder intervals, while initial manganese use (postdating ~74 ka) largely correlates with cold conditions.

Once we are in the variable conditions of MIS 3, other factors than seasonality and climate may affect occurrence

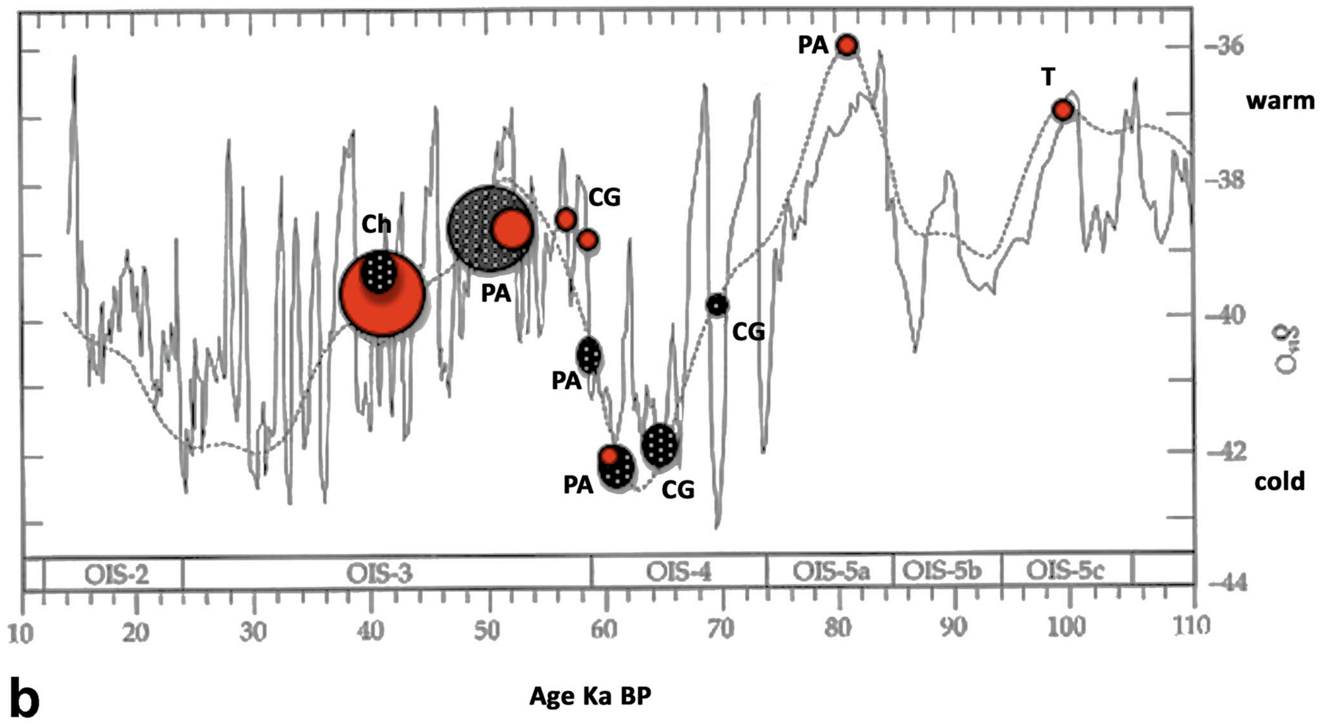

Figure 4. b) Pattern of (Neanderthal) pigment finds during Late Pleistocene (MIS 5–3) from selected sites (T=Tata; CG=Combe Grenal; PA=Pech de l'Azé sites; Ch=Châtelperronean sites; ochre= red circles; manganese=black circles).

of red ochre. General indications of substantial population growth in this period would, at least in the richest regions (e.g., Cantabria, Perigord), provide conditions for a ratchet effect, the fixation of behavioral innovations (Powell et al. 2009), in cultural traditions of pigment use, whether of manganese (initiated in the cold of MIS 4) or of red ochre.

Most Mousterian pigment finds in Europe (in sites from Spain to Russia) post-date 60 ka (Soressi and d'Errico 2007: 303). While no comprehensive inventory exists updating that provided by Wreschner (1983), two observations can be made—pigment use falls far short of the ubiquity documented in southern Africa from ~170 ka, and at a continental scale, red ochre continues to predominate. A significant qualification to this last inference concerns the Mousterian of Acheulean Tradition (MAT) in S.W. France, spanning the millennia either side of 50 ka, down to ~43 ka, where manganese is very commonly encountered (Demars 1992; Soressi and d'Errico 2007), a development from earlier (MIS 4) occurrences in the region. Copious use of red ochre, on a par with the scale of manganese use in the MAT of Layer 4 at Pech de l'Azé I (Soressi et al. 2008: 125–126), is first documented from Châtelperronean contexts ~42 ka (Couraud 1991; see also Carron et al. 2011; Harrold 1989: 696 and Table 33.8; Salomon 2009), roughly coincident with the arrival of modern humans. Climate was not warming overall during this period but went through rapid fluctuations. An overriding cultural factor could be contact between Neanderthal and immigrant moderns. Whether or not the Châtelperronean is viewed as an independent Neanderthal tradition (d'Errico et al. 1998; Zilhão 2006) or ascribed to cultural contact with moderns (Mellars 2005), the cosmetic signals predicted by the FCC model appear to have worked for the Neanderthals and cultural communication may have been possible between populations (cf. Chase 2007). What remains unexplained is the significant use of black manganese by classic Neanderthals (from MIS 4 onwards). At the moment, in line with the ST model, we cautiously propose that Neanderthals had a strong aversion to using red, quasi-menstrual signals during glacial cycles because stability of pair-bonds at such times would be paramount. Such a disposition could have tipped cultural traditions towards usage of black instead.

SUMMARY

Our preliminary findings are that the ST predictions are broadly met by the present Neanderthal pigment record for the Middle Pleistocene. For the Late Pleistocene, a more adequate data set is needed to test correlation of climate and pigment use. The lack of pigments in the glacial of MIS 8 and near absence from MIS 6, contrasting with fairly good representation from the more temperate conditions of MIS 7, seems to be a real phenomenon, not attributable to demography and archaeological visibility. At present, the absence in MIS 5.5 may be considered a sampling issue, but it clearly provides scope for refuting the prediction that red pigments should be present. On the other hand, the next occurrences of red pigments again appear to correlate with milder conditions—still within MIS 5 (Tata and Pech IV Layer J3b)—as do younger (MIS 3) occurrences at Combe Grenal. Another possible objection is that, if Neanderthal pigment use were fostered by relaxation of seasonality in warmer climes, we should find greater pigment use in southerly zones. This is clearly not the case in the Near East, where there are no well documented pigment occurrences associated with Neanderthals. In Mediterranean Europe, there may be no occurrences between Terra Amata and the Murcian sites, c. 50 ka. We currently have no answer to this absence of evidence.

This problem aside, one interpretation of the record is that ancestral Neanderthals developed the first, context-dependent phase of the FCC strategy but did not break through to habitual cosmetic ritual instituting symbolic gender and kinship, even in the Late Pleistocene. This would account for the sporadic nature of Neanderthal red ochre use. An alternative is that Neanderthals achieved the fully symbolic stage relatively late compared to moderns (within MIS 3), in places. The evidence from S.W. France and S.E. Spain centered on c. 50 ka suggests that in regions of high ecotonal diversity supporting fairly dense populations, stabilization of the cultural ratchet effect was achieved. This implies that seasonal constraints no longer put a brake on cultural transmission processes, allowing sexual selection to drive cosmetic ritual. Continuity into the Châtelperronean, despite apparent climate deterioration, supports this view.

From this perspective, the major difference between Neanderthal and African symbolic trajectories occurred particularly during MIS 6, when the lack of a ratchet effect prevented earlier stabilization of cosmetic strategies in Europe. By this time in Africa, ochre had already taken off culturally, as part of speciation.

CONCLUSION

Primate models of female reproductive synchrony and sexual signals lead us to expect that females will use these mechanisms to manipulate male behavior to optimize fitness, whether by confusing or concentrating paternity. Langur monkey populations provide a natural experiment for investigating the effects of these variables, producing different outcomes in mating systems and physiological signals such as visibility of menstruation, even within one species. Such primate case studies can inform our understanding of the strategies available to hominin females for increasing the numbers of males involved in breeding, leading to increased levels of male investment.

The main mechanisms for altering payoffs between male philanderers and male investors would be reproductive synchrony, effectively the degree of seasonal constraint on reproduction for hominin mothers; and, withholding accurate information from males on female fertility, either by hiding any signals of imminent fertility (menstruation), or by confusing such signals among coalitions of females. The latter Female Cosmetic Coalition model predicted that the early archaeological record of pigment use should track female reproductive costs as these increased with encephalization. The FCC model accounts for color selection, and timing of both initial use, and the shift to regular usage. However, this model alone does not distinguish between Eurasian and African records.

A seasonality thermostat model, combined with effects of cultural transmission, may explain the contrast in these records. Neanderthal mothers did not need regular ritual traditions because they had more reliable pair-bond stability, underpinned by their marked reproductive seasonality during glaciations. When seasonal constraints relaxed in warmer phases, they resorted to cosmetic deceptive sexual signals. By contrast, emerging African *Homo sapiens* developed those traditions because their pair-bonding was inherently less stable. They needed symbolic counter-strategies to resist male philanderers in tropical environments with less marked seasonality of reproduction. This led to an explosion of cosmetics use motored by sexual selection. By these ritual means, African foremothers mobilized men's hunting as mating effort rather than relying on parental effort. Ultimately, in terms of demographic factors of birth rate, and the social exploitation of the landscape, this proved the most successful strategy.

ACKNOWLEDGMENTS

Ian Watts thanks Michael Chazan for making it possible to examine material from Wonderwerk and Kathu Pan, allowing him to refer to preliminary findings ahead of scientific publication. Thanks also to David Morris and the McGregor Museum (Kimberley) for access to these collections.

ENDNOTES

1. To the extent that some of the proposed alternative uses of ochre are likely to rest on desiccant properties (e.g., hide preservation, hafting, external medicine, odor suppressant), red ochre may be more effective than yellow as the latter contain hydroxides of iron rather than haematite (an iron oxide). However, this would not address the finding that the reddest materials were most likely to bear use-wear (Watts 2010; see also Hodgskiss 2012). Judging from Rifkin's (2011) hide-working experiments, among the several red ochre/haematite samples tested, it was the co-presence of metal salts (sample 12), rather than relative iron content or color of the samples, that accounted for the small efficacy differences between the samples.
2. The ST model does not make any specific claim regarding forms of sexual division of labor (cf. Kuhn and Stiner 2006). It argues that pair-bonds become most stable when underpinned by reproductive seasonality during glacial cycles. Pair-bonded Neanderthal males are predicted to invest more in partners and offspring, and the investment pattern is expected to respond to reproductive and seasonal requirements. But this is not making any claim about foraging patterns of males or females, or how closely these resemble modern human hunter-gatherer economies.

REFERENCES

Aiello, Leslie C. and Catherine Key. 2002. Energetic consequences of being a *Homo erectus* female. *American Journal of Human Biology* 14: 551–565.

Alberts, Nienke. 2006. *Mechanisms and functions of oestrus desynchrony in Indian langur monkeys*. MS dissertation, University of London.

Alcorta, Candace. S. and Richard Sosis. 2005. Ritual, emotion, and sacred symbols. *Human Nature* 16: 323–359.

Alexander, Richard D. and K. M. Noonan. 1979. Concealment of ovulation, parental care, and human social evolution. In *Evolutionary Biology and Human Social Behavior*, Napoleon Chagnon and William Irons (eds.), pp. 436–

453, North Scituate, MA: Duxbury Press.

Anderson, C.M. 1992. Male investment under changing conditions among chacma baboons at Suikerbosrand. *American Journal of Physical Anthropology* 87: 479–496.

Antón, Susan C. 2003. A Natural History of *H. erectus*. *Yearbook of Physical Anthropology* 46: 126–170.

Bahn, Paul G. and Jean Vertut. 1988. *Images of the Ice Age.* London: Windward

Barham, Lawrence. 2002. Systematic pigment use in the Middle Pleistocene of south central Africa. *Current Anthropology* 43: 181–190.

Baker, Robin R. and Mark A. Bellis. 1993. Human sperm competition: ejaculate adjustment by males and the function of masturbation. *Animal Behaviour* 46: 861–885.

Barrickman, Nancy L., Meredith L. Bastian, Karin Isler, and Carel P. van Schaik. 2008. Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. *Journal of Human Evolution* 54: 568–590.

Beaumont, Peter. 1973. The ancient pigment mines of South Africa. *South African Journal of Science* 69: 140–146.

Beaumont, Peter. 1990a. Kathu. In *Guide to archaeological sites in the northern Cape*, P. Beaumont and D. Morris (eds.), pp. 75–100. Kimberley: McGregor Museum.

Beaumont, Peter. 1990b. Nooitgedacht 2 and Roseberry Plain 1. In *Guide to archaeological sites in the northern Cape*, P. Beaumont and D. Morris (eds.), pp. 4–6. Kimberley: McGregor Museum.

Beaumont, P. 2004. Canteen Koppje. In *Archaeology in the Northern Cape: Some key sites*, D. Morris, P. Beaumont (eds.), pp. 26–30. Kimberley: McGregor Museum.

Beaumont, Peter and J. Vogel. 2006. On a timescale for the past million years of human history in central South Africa. *South African Journal of Sciences* 102: 217–228.

Behm-Blancke, G. 1960. Altsteinzeitliche Rastplätze im Travertingebeit von Taubac, Weimar, Ehringsdorf. *Alt-Thüringen* 4: 2–246.

Behrensmeyer, A.K., N.E. Todd, R. Potts and G.B. McBinn. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278: 1589–1594.

Bellis, Mark A. and Robin R. Baker. 1990. Do females promote sperm competition? Data for humans. *Animal Behaviour* 40: 997–999.

Berndt, Ronald M. 1978. *Love Songs of Arnhem Land.* Chicago: University of Chicago Press.

Bischoff, J., R. Williams, R. Rosenbauer, A. Aramburu, J.L. Arsuaga, N. Garcia and G. Cuenca-Bescós. 2007. High-resolution U-series dates from the Sima de los Huesos hominids yields 600 +∞/-66 kyrs: Implications for the evolution of the early Neanderthal lineage. *Journal of Archaeological Science* 34: 763–770.

Boehm, Christopher. 2001. *Hierarchy in the Forest. The evolution of egalitarian behavior*. Cambridge, MA, and London: Harvard University Press.

Boesch, Christophe, G. Kohou, H. Nene, and Linda Vigilant. 2006. Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology* 130: 103–115.

Borries Carola and Andreas Koenig. 2000. Infanticide in Hanuman langurs: social organization, male migration, and weaning age. In *Infanticide by males and its implications*, Carel P. van Schaik and Charles H. Janson (eds.), pp. 99–122, Cambridge, UK: Cambridge University Press.

Borries, Carola, Kristin Launhardt, C. Epplen, J.T. Epplen, and Paul Winkler. 1999a. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society London B* 266: 901–904.

Borries, Carola, Kristin Launhardt, C. Epplen, J.T. Epplen and Paul Winkler. 1999b. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups—defence pattern, paternity and sexual behaviour. *Behavioural Ecology and Sociobiology* 46: 350–356.

Bouzouggar, A., Nick Barton, Marian Vanhaeren, Francesco d'Errico, S. Collcutt, Tom Higham, E. Hodge, S. Parfitt, E. Rhodes, J.-L. Schwenninger, Chris Stringer, E. Turner, S. Ward, A. Moutmir, and A. Stambouli. 2007. 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proceedings of the National Academy of Sciences USA* 104: 9964–9969.

Bowles, Samuel. 2006. Group competition, reproductive leveling, and the evolution of human altruism. *Science* 314: 1569–1572.

Boyd, Robert and Peter Richerson. 1992. Punishment allows the evolution of co-operation (or anything else) in sizeable groups. *Ethology and Sociobiology* 13: 191–196.

Boyd, Robert and Peter Richerson 2002. Group beneficial norms can spread rapidly in a structured population. *Journal of Theoretical Biology* 215: 287–296.

Boyd, Robert and Peter Richerson. 2005. Solving the puzzle of human cooperation. In *Evolution and Culture*, Steven Levinson (ed.), pp. 105–132. Cambridge, MA: MIT Press.

Bräuer, G. 2008. The origin of modern anatomy: By speciation or intraspecific evolution? *Evolutionary Anthropology* 17: 22–37.

Bräuer, G., C. Groden, F. Gröning, A. Kroll, K. Kupcyik, E. Mbua, A. Pommert, and T. Schiemann. 2004. Virtual study of the endocranial morphology of the matrix-filled cranium from Eliye Springs, Kenya. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology* 276A: 113–133.

Bronson, F.H. 1988. Seasonal regulation of reproduction in mammals. In *The Physiology of Reproduction,* E. Knobil and J. D. Neill (eds.), with L.L. Ewing, G.S. Greenwald, C.L. Markert, and D.W. Pfaff (assoc. eds.), pp. 1831–1871. New York: Raven.

Bronson, F.H. 1995. Seasonal variation in human reproduction: environmental factors. *Quarterly Review of Biology* 70: 141–164.

Burkart, Judith M., Sarah Blaffer Hrdy, and Carel P. van Schaik. 2009. Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology* 18: 175–186.

Burne, J. 1995. Love in a cold climate dents monkeys' macho image. *New Scientist* Feb 25, p.15.

Butzer, K. 1980. Comment on Wreshner: red ochre and human evolution. *Current Anthropology* 21: 635.

Byrne, Richard and Andrew Whiten (eds.). 1988. *Machiavellian Intelligence. Social expertise and the evolution of intellect in monkeys, apes, and humans.* Oxford: Clarendon.

Cachel, Susan. 1997. Dietary shifts and the European Upper Palaeolithic transition. *Current Anthropology* 38, 579–603.

Calame-Griaule, Geneviève. 1965. *Ethnologie et langage. La parole chez les Dogon.* Paris: Gallimard.

Carnes, L.M., Charles L. Nunn and R.J. Lewis. 2011. Effects of the distribution of female primates on the number of males. *PLoS One* 6 (5): e19853. doi:10.1371/ journal.pone.0019853

Caron, François., Francesco d'Errico, Pierre del Moral, Frédéric Santos, and João Zilhão 2011. The reality of Neandertal symbolic behavior at the Grotte du Renne, Arcy-sur-Cure, France. *PLoS ONE* 6 (6): e21545, doi:10.1371/ journal.pone.0021545.

Cerling, T.E., J.R. Bowman and J.R. O'Neil 1988. An isotopic study of a fluvial-lacustrine sequence: The Plio-Pleistocene Koobi-Fora Sequence, East Africa. *Palaeogeography, Palaeoclimatology and Palaeoecology* 63: 335–356.

Chase, Phillip G. 2007. The significance of 'acculturation' depends on the meaning of 'culture'. In *Rethinking the Human Revolution,* Paul Mellars, Katie Boyle, Ofer Bar-Yosef, and Chris Stringer (eds.), pp. 55–65. Cambridge, UK: McDonald Institute Monographs.

Churchill, Steven E. 1998. Cold adaptation, heterochrony, and neanderthals. *Evolutionary Anthropology* 7: 46–61.

Churchill, Steven E. 2006. Bioenergetic perspectives on neanderthal thermoregulatory and activity budgets. In *Neanderthals revisited: new approaches and perspectives*, K. Harvati and T. Harrison (eds.), pp. 113–134. New York: Springer.

Churchill, Steven E., Lee Berger, Adam Hartstone-Rose, and B. Headman Zondo. 2012. Body size in African Middle Pleistocene *Homo*. In *African genesis: Perspectives on hominin evolution*, S. Reynolds and A. Gallagher (eds.), pp. 319–346. Cambridge, UK: Cambridge University Press.

Cichy, K. 1997. *Male-infant interactions and adult male social strategies in* Macaca fascicularis. PhD dissertation, University of Southern Illinois.

Clutton-Brock, Tim H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London* B 236: 339–372.

Coltorti, M., G. Feraud, A. Marzoli, C. Peretto, T. Ton-That, P. Voinchet, J.-J. Bahain, A. Minelli, and U. Thun Hohenstein. 2005. New ^{40}Ar/^{39}Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quarternary International* 131: 11–22.

Condon, R.G. 1991. Birth seasonality, photoperiod, and social change in the central Canadian Arctic. *Human Ecology* 19, 287–321.

Couraud, C. 1991. Les pigments des grottes D'Arcy-sur-Cure (Yonne). *Gallia Préhistoire* 33: 17–52.

Cremaschi, M. and C. Peretto. 1988. Le Paléolithique inférieur de la plaine du Pô. *L'Anthropologie* 92: 643–682.

Dayet, L., P.J. Texier, F. Daniel, and G. Porraz. 2013. Ochre resources from the Middle Stone Age sequence of Diepkloof Rock Shelter, Western Cape, South Africa. *Journal of Archaeological Science* 40: 3492–3505.

de Lumley, Henry. 1966. Les fouilles de Terra Amata à Nice. *Bulletin du Musée d'Anthropologie Préhistorique de Monaco* 13 : 29–51.

Delpech, F. and F. Prat. 1995. Nouvelles observations sur les faunes Acheuléennes de Combe Grenal (Dommes, Dordogne). *Paléo* 7 : 123–137.

Demars, P.-Y. 1992. Les colorants dans le Moustérien du Périgord: l'apport des fouilles de F. Bordes. *Préhistoire Ariegeoise* 47: 185–194.

De Miguel, C. and M. Henneberg. 2001. Variation in hominid brain size: how much is due to method? *Homo* 52: 3–58.

d'Errico, Francesco. 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology* 12: 188–202.

d'Errico, Francesco, Chris Henshilwood, Marian Vanhaeren, and Karen van Niekerk. 2005. *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *Journal of Human Evolution* 48: 3–24.

d'Errico, Francesco, Hélène Salomon, Colette Vignaud, and Chris Stringer. 2010. Pigments from the Middle Palaeolithic levels of Es-Skhul (Mount Carmel, Israel). *Journal of Archaeological Sciences* 37: 3099–3110.

d'Errico, Francesco and Chris Stringer. 2011. Evolution, revolution or saltation scenario for the emergence of modern culture. *Philosophical Transactions of the Royal Society, Series B* 366: 1060–1069.

d'Errico, Francesco, João Zilhão, M. Julien, D. Baffier, and J. Pelegrin. 1998. Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation. *Current Anthropology* 39 (supplement): S1–S44.

Dibble, Harold, F. Berna, P. Goldberg, Shannon P. McPherron, L. Niven, D. Sandgathe, I. Théry-Parisot, and A. Turq 2009. A preliminary report on Pech de l'Azé IV, Layer 8 (Middle Paleolithic, France). *PaleoAnthropology* 2009: 182–219.

Dibble, Harold and Shannon P. McPherron. 2006. The missing Mousterian. *Current Anthropology* 47: 777–803.

Dunbar, Robin I.M. 1988. *Primate Social Systems*. London and Sydney:Croom Helm.

Dunbar, Robin I.M. 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 20: 469–493.

Dunbar, Robin I.M. 1998. The social brain hypothesis. *Evolutionary Anthropology* 6: 178–191.

Ellison, Peter T. 1994. Advances in human reproductive ecology. *Annual Review of Anthropology* 23: 255–275.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. *Science* 197: 215–223.

Erdal, David and Andrew Whiten. 1996. Egalitarianism and machiavellian intelligence in human evolution. In *Modelling the Early Human Mind,* Paul Mellars and Kathleen Gibson (eds.), pp. 139–150. Cambridge, UK: McDonald Institute Monographs.

Falguères, C., Y. Yokoyama, and J.-P. Quaegebeur.1991. Datation par la resonance de spin électronique (E.S.R.)

de sédments quaternaires. *Cahiers du Quaternaires* 16: 39–52.

Finlayson, Clive. 2004. *Neanderthals and modern humans. An ecological and evolutionary perspective*. Cambridge, UK: Cambridge University Press.

Foley, Robert A. 1993. The influence of seasonality on hominid evolution. In *Seasonality and Human Ecology*, S.J. Ulijaszek and S.S. Strickland (eds.), pp. 15–64. Cambridge, UK: Cambridge University Press.

Foley, Robert A. and Charles M. Fitzgerald. 1996. Is reproductive synchrony an evolutionarily stable strategy for hunter-gatherers? *Current Anthropology* 37: 539-545.

Gavrilets, Sergey. 2012. Human origins and the transition from promiscuity to pair-bonding. *Proceedings of the National Academy of Sciences USA* 109: 9923–9928.

Gilby, Ian C., Lynn E. Eberly, Lilian Pintea, and Anne E. Pusey. 2006. Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii. Animal Behaviour* 72: 169–180.

Gintis, Herbert, Eric A. Smith and Samuel Bowles. 2001. Cooperation and costly signaling. *Journal of Theoretical Biology* 213: 103–119.

Gintis, Herbert, Samuel Bowles, Robert Boyd, and Ernst Fehr. 2003. Explaining altruistic behavior in humans. *Evolution and Human Behavior* 24: 153–172.

Grammer, Karl. 1996. The human mating game: The battle of the sexes and the war of signals. Paper presented at the Human Behavior and Evolution Society annual conference, Evanston, June 29.

Grün, Rainer and Peter Beaumont. 2001. Border Cave revisited: a revised ESR chronology. *Journal of Human Evolution* 40: 467–482.

Grün, Rainer, J. Brink, N. Spooner, L. Taylor, Chris Stringer, R. Franciscus, and A. Murray. 1996. Direct dating of Florisbad hominid. *Nature* 382: 500–501.

Hardy Bruce L. and Marie-Hélène Moncel. 2011. Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125–250,000 Years Ago. *PLoS ONE* 6(8): e23768. doi:10.1371/journal.pone.0023768

Harpending, Henry C. and Pat Draper. 1986. Selection against human family organization. In *On evolutionary anthropology: essays in honour of Harry Hoijer 1983,* B.J. Williams (ed.), pp. 100–107. Undena: UCLA.

Harrold, F.B. 1989. Mousterian, Châtelperronean and early Aurignacian in western Europe: continuity or discontinuity? In *The Human revolution: behavioral and biological perspectives in the origins of modern humans,* Paul Mellars and Chris B. Stringer (eds.), pp. 677–713. Edinburgh: Edinburgh University Press.

Harvati, Katerina, Chris Stringer, Rainer Grün, M. Aubert, P. Allsworth-Jones, and C. Adebayo Folorunso. 2011a. The Later Stone Age calvaria from Iwo Eleru, Nigeria: Morphology and chronology. *PLoS One* 6: e24024. doi:10.1371/journal.pone.0024024.

Harvati, Katerina, Chris Stringer, and P Karkanas. 2011b. Multivariate analysis and classification of the Apidima 2 cranium from Mani, Southern Greece. *Journal of Human Evolution* 60: 246–250.

Hartwig-Scherer, Sigrid. 1994. Body weight prediction in fossil *Homo*. *Courier Forschungsinstitut Senckenberg* 171: 267–279.

Hausmann, R. and K. Brunnacker. 1988. U-series dating of Middle European travertine's. In *L'Homme de Néandertal 1. La chronologie*, M. Otte (ed.), pp. 45–51. Liège: University of Liège Press.

Hawkes, Kristen, James F. O'Connell, Nicholas G. Blurton Jones, Helen Alvarez, and Eric L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences USA* 95: 1336–1339.

Heistermann, Michael, Thomas Ziegler, Carel P. van Schaik, Kristin Launhardt, Paul Winkler, and J.K. Hodges. 2001. Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs. *Proceedings of the Royal Society of London* 268: 2445–2451.

Henrich, Joseph, Samuel Bowles, Robert Boyd, A. Hopfensitz, Peter Richerson, K. Sigmund, Eric A. Smith, F. Weissing, and H. Peyton Young. 2003. The cultural and genetic evolution of human cooperation. In *Genetic and cultural evolution of cooperation*, Peter Hammerstein (ed.), pp. 445–468. Cambridge, MA: MIT Press.

Henrich, Joseph and Robert Boyd. 2001. Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative endeavours. *Journal of Theoretical Biology* 208: 79-89.

Henrich, Joseph, R. McElreath, A. Barr, Jean Ensminger, C. Barrett, A. Bolyanatz, J. Cardenas, Michael Gurven, E. Gwako, N. Henrich, C. Lesorogol, Frank Marlowe, D. Tracer, and J. Ziker. 2006. Costly punishment across human societies. *Science* 312: 1767–1770.

Henshilwood, Chris S., Francesco d'Errico, and Ian Watts. 2009. Engraved ochres from Middle Stone Age levels at Blombos Cave, South Africa. *Journal of Human Evolution* 57: 27–47.

Henshilwood, Chris, Francesco d'Errico, Karen van Niekerk, Y. Coquinot, Zenobia Jacobs, S.-E. Lauritzen, M. Menu, and R. García-Moreno. 2011. A 100,000-year-old ochre-processing workshop at Blombos Cave, South Africa. *Science* 334: 219–222.

Henshilwood, Chris S., Francesco d'Errico, Royden Yates, Zenobia Jacobs, Chantal Tribolo, Geoff A.T. Duller, Norbert Mercier, Judith C. Sealy, Helene Valladas, Ian Watts, and Ann G. Wintle. 2002. Emergence of modern human behavior: Middle Stone Age engravings from South Africa. *Science* 295: 1278–1280.

Henshilwood, Chris S., Judith C. Sealy, Royden Yates, Kathryn Cruz-Uribe, Paul Goldberg, Frederick E. Grine, Richard G. Klein, Cedric Poggenpoel, Karen van Niekerk, and Ian Watts. 2001. Blombos Cave, Southern Cape, South Africa: Preliminary report on the 1992–1999 excavations of the Middle Stone Age levels. *Journal of Archaeological Science* 28: 421–448.

Hodgskiss, Tamaryn. 2012. An investigation into the properties of the ochre from Sibudu, KwaZulu-Natal, South Africa. *Southern African Humanities* 24: 99–120.

Holliday, Trenton W. 1997. Postcranial evidence of cold adaptation in European neandertals. *Americal Journal of Physical Anthropology*. 104: 245-258.

Hovers, Erella, Shimon Ilani, Ofer Bar-Yosef, and Bernard Vandermeersch. 2003. An early case of color symbolism. Ochre use by modern humans in Qafzeh Cave. *Current Anthropology* 44: 491–522.

Howell, F. Clark. 1966. Observations on the earlier phases of the European Lower Paleolithic. *American Anthropologist* 68: 88–201.

Hrdy, Sarah Blaffer. 1981. *The Woman that Never Evolved.* Cambridge, MA: Harvard University Press.

Hrdy, Sarah Blaffer. 2009. *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, MA: Harvard University Press.

Huo, Jianying. 2004. http://www.chinatoday.com.cn/English/e200411/p60.htm.

Irons, William G. 2001. Religion as hard-to-fake sign of commitment. In *Evolution and the Capacity for Commitment*, Randolph M. Nesse (ed.), pp. 292–309. New York: Russell Sage Foundation.

Kaplan, Hillard S., Kim Hill, Jane B. Lancaster, and A. Magdalena Hurtado. 2000. A theory of human life history evolution: diet, intelligence and longevity. *Evolutionary Anthropology* 9: 156–185.

Kappelman, J. 1996. The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution* 30: 243–276.

Key, Catherine A. 1998. *Cooperation, paternal care and the evolution of social groups*. PhD dissertation, University of London.

Key, Catherine A. 2000. The evolution of human life history. *World Archaeology* 31: 329–350.

Key, Catherine A. and Leslie C. Aiello. 1999. The evolution of social organization. In *The Evolution of Culture*, Robin I.M. Dunbar, Chris Knight, and Camilla Power (eds.), pp. 15–33. Edinburgh: Edinburgh University Press.

Key, Catherine A. and Leslie C. Aiello. 2000. A prisoner's dilemma model of the evolution of paternal care. *Folia Primatologica* 71: 77–92.

Klein, Richard G. 1995. Anatomy, behaviour and modern human origins. *Journal of World Prehistory* 9: 167–198.

Klein, Richard, G. Avery, K. Cruz-Uribe, and T. Steele. 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulian artifacts at Elandsfontein, Western Cape Province, South Africa. *Journal of Human Evolution* 52: 164–186.

Kneblova, V. 1958. The interglacial flora in Ganovce travertines in Eastern Slovakia (Czechoslavakia). *Acta Biologica* Cracov 1: 1–5.

Knight, Chris. 1991. *Blood Relations. Menstruation and the origins of culture*. New Haven and London: Yale University Press.

Knight, Chris, Camilla Power, and Ian Watts. 1995. The human symbolic revolution: a Darwinian account. *Cambridge Archaeological Journal* 5: 75–114.

Knowlton, Nancy. 1979. Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. *Animal Behaviour* 27: 1022–1033.

Koenig, Andreas and Carola Borries. 2001. Socioecology of Hanuman langurs: the story of their success. *Evolutionary Anthropology* 10: 122–137.

Koenig Andreas, Carola Borries, Mukesh K. Chalise, and Paul Winkler. 1997. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of the Zoological Society of London* 243: 215–235.

Kuhn, Steven L. and Mary C. Stiner. 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. *Current Anthropology* 47: 953–980.

Kutsukake, N. and Charles L. Nunn. 2006 Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. *Behavioral Ecology and Sociobiology* 60: 695–706.

Launhardt, Kristin, Carola Borries, C. Hardt, J.T. Epplen, and Paul Winkler. 2001. Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Animal Behaviour* 61: 53–64.

Lee, S.-H. and Milford Wolpoff. 2003. The pattern of evolution in Pleistocene human brain size. *Paleobiology* 29: 186–196.

Lewis, Jerome. 2002. *Forest hunter-gatherers and their world*. PhD dissertation, University of London.

Little, Katherine, Volker Sommer, and Mike Bruford. 2002. Genetics and relatedness: a test of hypotheses using wild Hanuman langurs, *Presbytis entellus*. Abstracts, XIXth Congress, International Primatological Society, Beijing, Aug 4-9, 2002.

Lombard, Marlize. 2007. The gripping nature of ochre: The association of ochre with Howiesons Poort adhesivies and Later Stone Age mastics from South Africa. *Journal of Human Evolution* 53: 406–419.

Macdonald, Katharine and Wil Roebroeks. 2005. Comment on Kuhn and Stiner. *Current Anthropology* 47: 966–967.

Macdonald, Katharine, Wil Roebroeks, and Alexander Verpoorte. 2009. An energetics perspective on the Neanderthal record. In *The Evolution of Hominid Diets: Integrating approaches to the study of Palaeolithic subsistence*, Jean-Jacques Hublin and Micahel P. Richards (eds.), pp. 211–220. Berlin: Springer.

Mackay, A. and A. Welz. 2008. Engraved ochre from a Middle Stone Age context at Klein Kliphuis in the Western Cape of South Africa. *Journal of Archaeological Science* 35: 1521–1532.

Manega, P. 1993. *Geochronology, geochemistry and isotopic study of the Plio-Pleistocene hominid sites and the Ngorongoro volcanic highland in Northern Tanzania*. Ph.D., University of Colorado.

Manzi, G., D. Magri, S. Milli, M. Palombo, V. Margari, V. Celiberti, M. Barbieri, M. Barbieri, R. Melis, M. Rubini, M. Ruffo, B. Saracino, P. Tzedakis, A. Zarattini, and I. Biddittu. 2010. The new chronology of the Ceprano calvarium (Italy). *Journal of Human Evolution* 59: 580–585.

Marean, Curtis W., M. Bar-Matthews, J. Bernatchez, E. Fisher, P. Goldberg, A.I.R. Herries, Zenobia Jacobs, A. Jerardino,

P. Karkanas, T. Minichillo, P.J. Nilssen, E. Thompson, Ian Watts, and H.M. Williams. 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449: 905–908.

Marlowe, Frank W. 2001. Male contribution to diet and female reproductive success among foragers. *Current Anthropology* 42: 755–760.

Marlowe, Frank W. 2004. Is human ovulation concealed? Evidence from conception beliefs in a hunter-gatherer society. *Archives of Sexual Behavior* 33: 427–432.

Marshack, Alexander. 1976. Implications of the paleolithic symbolic evidence for the origin of language. *Current Anthropology* 17: 274–284.

Marshack, Alexander. 1981. On paleolithic ochre and the early uses of colour and symbol. *Current Anthropology* 22: 188–191.

Martin, Robert D. 1992. Female cycles in relation to paternity in primate societies. In. *Paternity in primates: genetic tests and theories*, Robert. D. Martin, A.F. Dixson, and E.J. Wickings (eds.), pp. 238–274. Basel: Karger.

Mason, R. 1957. The Transvaal Middle Stone Age and statistical analysis. The *South African Archaeological Bulletin* 12: 119–137.

McBrearty, Sally and Alison Brooks. 2000. The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39: 453–563.

McCown, T. 1937 Mugharet es-Skhul: description and excavations. In *The Stone Age of Mount Carmel*, D. Garrod and D. Bate (eds.), pp. 91–107. Oxford: Clarendon Press.

McDougall, I., F. Brown, and John Fleagle. 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Natur*e 433: 733–736.

McHenry, Henry M. 1996. Sexual dimorphism in fossil hominids and its socioecological implications. In The *Archaeology of Human Ancestry*, James Steele and Stephen Shennan (eds.), pp. 91–109. London: Routledge.

Mellars, Paul. 1996. *The Neanderthal Legacy*. Princeton, NJ: Princeton University Press.

Mellars, Paul. 2005. The impossible coincidence: a single-species model for the origins of modern human behaviour in Europe. *Evolutionary Anthropology* 14: 12–27.

Miller, G., J.M. Tybur, and B.D. Jordan. 2007. Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evolution and Human Behavior* 28: 375–381.

Mishra, S. 1992. The age of the Acheulian in India: new evidence. *Current Anthropology* 33: 325–328.

Mitani John C., J. Gros-Louis, and J.H. Manson. 1996. Number of males in primate groups: comparative tests of competing hypotheses. *American Journal of Primatology* 38: 315–332.

Morin, Eugène and Véronnique Laroulandie. 2012. Presumed symbolic use of diurnal raptors by Neanderthals. *PLoS One* 7(3): 1–5, e32856. doi:10.1371/journal.pone.0032856.

Mussi, M. 2007. Women of the middle latitudes: the earliest peopling of Europe from a female perspective. In *Guts and Brains: an integrative approach to the hominin record*, W. Roebroeks (ed.), pp. 165–184. Leiden: Leiden University Press.

Nowak, Martin A. and Karl Sigmund. 2005. Evolution of indirect reciprocity. *Nature* 437: 1291–1298.

Nunn, Charles L. 1999 The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology* 46: 1–13.

O'Connell, James F., Kristen Hawkes, and Nicholas G. Blurton Jones. 1999. Grandmothering and the evolution of *Homo erectus. Journal of Human Evolution* 36: 461-485.

Obermaier, H. 1925. Castillo-Hohle. *Eberts Reallexikon der Vorgeschichte* Band II: 290–292. Berlin: W. de Gruyter.

Opie, Kit and Camilla Power. 2008. Grandmothering and female coalitions: a basis for matrilineal priority? In *Early Human Kinship. From sex to social reproduction*, Nick J. Allen, Hilary Callan, Robin Dunbar, and Wendy James (eds.), pp. 168–186. Oxford: Blackwell.

Ostner, Julia, Mukesh K. Chalise, Andreas Koenig, Kristin Launhardt, Julia Nikolei, Doris Podzuweit, and Carola Borries. 2006. What Hanuman langur males know about female reproductive status. *American Journal of Primatology* 68: 701–712.

Ostner, Julia, Charles L. Nunn, and Oliver Schülke. 2008. Female reproductive synchrony predicts skewed paternity across primates. *Behavioral Ecology* 19: 1150–1158.

Pappu, S., Y. Gunnell, K. Akhilesh, R. Braucher, M Taieb, F. Demory, and N. Thouveny. 2011. Early Pleistocene presence of Acheulian hominins in South India. *Science* 331: 1596–1599.

Paul, Andreas. 1997. Breeding seasonality affects the association between dominance and reproductive success in non-human male primates. *Folia Primatologica* 68: 344–349.

Peresani, M., I. Fiore, M. Gala, M. Romandini, and A. Tagliacozzo. 2011. Late Neandertals and the intentional removal of feathers as evidenced from bird-bone taphonomy at Fumane 44 ky BP, Italy. *Proceedings of the National Academy of Sciences USA* 108: 3888–3893.

Ponce de León, M.S., L. Golovanova, V. Doronichev, G. Romanova, T. Akazawa, O. Kondo, H. Ishida, and C.P.E. Zollikofer. 2008. Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceedings of the National Academy of Sciences USA* 105: 13764–13768.

Porat, N., Michael Chazan, Rainer Grün, M. Aubert, V. Eisenmann, and L. Horwitz. 2010. New radiometric ages for the Fauresmith industry from Kathu Pan, southern Africa: implications for the Earlier to Middle Stone Age transition. *Journal of Archaeological Science* 37: 269–283.

Potts, M. and R. Short. 1999. *Ever Since Adam and Eve. The evolution of human sexuality*. Cambridge, UK: Cambridge University Press.

Potts, R. 1998. Environmental hypotheses of hominin evolution. *Yearbook of Physical Anthropology* 41: 93–136

Potts, R., A. Behrensmeyer, A. Deino, P. Ditchfield, and J. Clark. 2004. Small mid-Pleistocene hominin associated with East African Acheulian technology. *Science* 305: 75–78.

Powell, Adam, Stephen Shennan, and Mark G. Thomas. 2009. Late Pleistocene demography and the appearance of modern human behavior. *Science* 324: 1298–1301 DOI: 10.1126/science.1170165

Power, Camilla. 1999. Beauty magic: the origins of art. In *The Evolution of Culture. An interdisciplinary view,* Robin Dunbar, Chris Knight and Camilla Power (eds.), pp. 92–112. Edinburgh: Edinburgh University Press.

Power, Camilla. 2001. *Beauty magic: deceptive sexual signalling and the evolution of ritual*. PhD dissertation, University of London.

Power, Camilla. 2009. Sexual selection models for the evolution of language: why they should be reversed. In *The Cradle of Language*, Rudolf Botha and Chris Knight (eds.), pp. 257–280. Oxford: Oxford University Press.

Power, Camilla and Leslie C. Aiello. 1997. Female protosymbolic strategies. In *Women in Human Evolution,* Lori D. Hager (ed.), pp. 153–171. New York and London: Routledge.

Power, Camilla, Catherine Arthur, and Leslie C. Aiello. 1997. On seasonal reproductive synchrony as an evolutionarily stable strategy in human evolution. *Current Anthropology* 38: 88–91.

Power, Camilla and Ian Watts. 1996. Female strategies and collective behaviour: The archaeology of earliest *Homo sapiens sapiens*. In *The Archaeology of Human Ancestry,* James Steele and Stephen Shennan (eds.), pp. 306–330. London and New York: Routledge.

Power, Camilla and Ian Watts. 1997. The woman with the zebra's penis: gender, mutability and performance. *Journal of the Royal Anthropological Institute* n.s. 3: 537–560.

Power, Camilla and Ian Watts. 1999. First gender, wrong sex. In *Those who play with fire: gender, fertility and transformation in East and Southern Africa*, Henrietta Moore, Todd Sanders, and Bwire Kaare (eds.), pp. 101–132. London and New Brunswick (NJ): Athlone Press.

Rae, Todd C., Una Strand Viðarsdóttir, Nathan Jeffery, and A. Theodore Steegmann, Jr. 2006. Developmental response to cold stress in cranial morphology of *Rattus*: implications for the interpretation of climatic adaptation in fossil hominins. *Proceedings of the Royal Society of London B* 273: 2605–2610.

Rajpurohit, Lal Singh and Volker Sommer. 1993. Juvenile male emigration from one-male troops in Hanuman langurs (*Presbytis entellus*)—a long-term study of intrasexual competition. In *Juvenile primates: life history, development, and behavior*, Michael Pereira and Lynn Fairbanks (eds.), pp. 86–103. New York: Oxford University Press.

Rajpurohit, Lal Singh, Volker Sommer, and Surendra Mal Mohnot. 1995. Wanderers between harems and bachelor bands: male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. *Behaviour* 132: 255–299.

Reed, Kaye E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution* 32: 289–322.

Reed, Kaye E. and Jennifer L. Fish. 2005. Tropical and temperate seasonal influences on human evolution. In *Seasonality in Primates. Studies of living and extinct human and non-human primates*, Diane K. Brockman and Carel P. van Schaik (eds.), pp. 489–518. Cambridge, UK: Cambridge University Press.

Richerson, Peter, Robert Boyd, and Joseph Henrich. 2003. The cultural evolution of cooperation. In *The genetic and cultural evolution of cooperation*, Peter Hammerstein (ed.), pp. 357–388. Cambridge, MA: MIT Press.

Richter, D., Harold Dibble, P. Goldberg, Shannon McPherron, L. Niven, D. Sandgathe, S. Talamo and A. Turq. 2013. The late Middle Palaeolithic in Southwest France: New TL dates for the sequence of Pech de l'Azé IV. *Quaternary International* 294: 160–167.

Ridley Mark. 1986. The number of males in a primate troop. *Animal Behaviour* 34: 1848–1858.

Rifkin, Riaan. 2011. Assessing the efficacy of red ochre as a prehistoric hide-tanning ingredient. *Journal of African Archaeology* 9: 131–158.

Rightmire, G. Philip. 1996. The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? *Journal of Human Evolution*, 31: 21–39.

Rightmire, G. Philip. 2001. Patterns of hominid evolution and dispersal in the Middle Pleistocene. *Quaternary International* 75: 77–84.

Rightmire, G. Philip. 2004. Brain size and encephalization in Early to Mid-Pleistocene *Homo*. *American Journal of Physical Anthropology* 124: 109–123.

Rightmire, G. Philip. 2009 Middle and late Pleistocene hominins in Africa and Southwest Asia. *Proceedings of the National Academy of Sciences USA* 106: 16046–16050.

Robson, Shannen L. and Bernard Wood. 2008. Hominin life history: Reconstruction and evolution. *Journal of Anatomy* 212: 394–425.

Roebroeks, Wil, M. Sier, T. Nielsen, D. De Loecker, J. Parés, C. Arps, and H. Mücher. 2012. Use of red ochre by early Neandertals. *Proceedings of the National Academy of Sciences USA* 109: 1889–1894.

Roebroeks, Wil and Alexander Verpoorte. 2009. A "language-free" explanation for differences between the European Middle and Upper Palaeolithic record. In *The Cradle of Language*, Rudolf Botha and Chris Knight (eds.), pp. 150–166. Oxford: Oxford University Press.

Ruff, Christopher B. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearbook of Physical Anthropology* 37: 65–107.

Ruff, Christopher B., Erik Trinkaus, and Trenton W. Holliday. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387: 173–176.

Sadleier, R.M.S. 1969. *The ecology of reproduction in wild and domestic animals.* London: Methuen.

Salomon, Hélène. 2009. *Les matières colorantes au début du Paléolithique supérieur: sources, transformations and fonctions*. PhD dissertation, University of Bordeaux 1.

Salomon, Hélène, C. Vignaud, Y. Coquinot, L. Beck, Chris Stringer, D. Strivay, and Francesco d'Errico. 2012. Selection and heating of colouring materials in the Mousterian level of Es-Skhul (c. 100 000 years BP, Mount Carmel, Israel). *Archaeometry* 54: 698–722.

San-Juan, C. 1990. Les matières colorantes dans les collections du Musée National de Préhistoire des Eyzies. *Paléo* 2:229–242.

Sandgathe, D., Harold Dibble, P. Goldberg, Shannon McPherron, A. Turq, L. Niven and J. Hodgkins. 2011. On the role of fire in Neandertal adaptations in Western Europe: evidence from Pech de l'Azé IV and Roc de Marsal, France. *PaleoAnthropology* 2011: 216–242.

Schwartz, Jeffrey H., Ian Tattersall, and Jeffrey T. Laitman 1999. New thoughts on neanderthal behaviour: evidence from nasal morphology. In *Hominid Evolution. Lifestyles and survival strategies*, H. Ullrich (ed.), pp. 166–186. Gelsenkirchen/Schwelm: Edition Archaea.

Scott, Beccy, and Nick Ashton. 2011. The Early Middle Palaeolithic: The European context. In *The Ancient Human Occupation of Britain*, Nick Ashton, Simon Lewis, and Chris Stringer (eds.), pp. 91–112. Developments in Quaternary Science 14. Amsterdam: Elsevier.

Shultz, Susanne, Emma Nelson, and Robin Dunbar. 2012. Hominin cognitive evolution: identifying patterns and processes. *Philosophical Transactions of the Royal Society B* 367: 2130–2140.

Slimak, L., J. Lewis, E. Crégut-Bonnoure, L. Metz, V. Ollivier, P. André, J. Chrzavzez, Y. Giraud, M. Jeannet, and F. Magnin. 2010. Le Grand Abri aux Puces, a Mousterian site from the Last Interglacial: Paleogeography, paleoenvironment, and new excavation results. *Journal of Archaeological Science* 37: 2747–2761.

Sillén-Tullberg, Birgitta and Anders P. Møller. 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *American Naturalist* 141: 1–25.

Smith, Tanya M., Paul Tafforeau, Donald J. Reid, Joane Pouech, Vincent Lazzari, John P. Zermeno, Debbie Guatelli-Steinberg, Anthony J. Olejniczak, Almut Hoffman, Jakov Radovčić, Masrour Makaremi, Michel Toussaint, Chris Stringer, and Jean-Jacques Hublin. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proceedings of the National Academy of Sciences USA* 107: 20923–20928. (doi: 10.1073/pnas.1010906107).

Snodgrass, J.J. and W.R. Leonard. 2009. Neandertal energetics revisited: insights into population dynamics and life history evolution**.** *PaleoAnthropology*: 220–237.

Sommer, Volker. 1989. Infant mistreatment in langur monkeys—sociobiology tackled from the wrong end? In *The sociobiology of sexual and reproductive strategies in animals and humans,* Anne E.O. Rasa, Christian Vogel, and Eckart Voland (eds.), pp. 110–127. London: Chapman and Hall.

Sommer, Volker. 1994. Infanticide among langurs of Jodhpur—testing the sexual selection hypothesis with a long-term record. In *Infanticide and Parental Care*, Stefano Parmigiani and Fred vom Saal (eds.), pp. 155–198. New York: Harwood Academic.

Sommer, Volker. 1996. *Heilige Egoisten. Die Soziobiologie indischer Tempelaffen*. Munich: CH Beck.

Sommer, Volker and Domingo Mendoza-Granados. 1995. Play as indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethology* 99: 177–192.

Sommer, Volker and Lal Singh Rajpurohit. 1989. Male reproductive success in harem troops of Hanuman langurs (*Presbytis entellus*). *International Journal of Primatology* 10: 293–317.

Sommer, Volker, Arun Srivastava, and Carola Borries. 1992. Cycles, sexuality, and conception in free-ranging female langurs (*Presbytis entellus*). *American Journal of Primatology* 28 (supplement): S1–27.

Sørensen, B. 2009. Energy use by Eem Neanderthals. *Journal of Archaeological Science* 36: 2201–2205.

Sorenson, Mark V. and William R. Leonard. 2001. Neandertal energetics and foraging efficiency. *Journal of Human Evolution* 40 : 483–495.

Soressi, Marie and Francesco d'Errico. 2007. Pigments, gravures, parures : les comportements symboliques controversés des Néandertaliens. In *Les Néandertaliens. Biologie et cultures*, Bernard Vandermeersch and B. Maureille (eds.), pp. 297–309. Documents préhistoriques 23. Paris, Éditions du CTHS.

Soressi, Marie, W. Rendu, J.-P. Texier, E. Claud, L. Daulny, Francesco d'Errico, V. Laroulandie, B. Maureille, M. Niclot, S. Schwortz, and A-M. Tillier. 2008. Pech de l'Azé I (Dordogne, France): nouveau regard sur un gisement moustérien de tradition acheuléenne connu depuis le XIX^{e} siècle. In *Les sociétés Paléolithiques d'un grand Sud-Ouest de la France: nouveaux gisements, nouvelles méthodes, nouveaux résultats*, Jacques Jaubert, J.-G. Bordes, and I. Ortega (eds.), pp. 95–132. Actes des journées décentralisées de la SPF des 24–25 novembre 2006, Mémoire de la Société préhistorique française 47. Université Bordeaux.

Spencer, L.M. 1997. Dietary adaptations of Plio-Pleistocene bovidae: implications for hominid habitat use. *Journal of Human Evolution* 32: 201–228.

Speth, John D. 1987. Early hominid subsistence strategies in seasonal habitats. *Journal of Archaeological Science* 14: 13–29.

Speth, John D. 1989. Early hominid hunting and scavenging: the role of meat as an energy source. *Journal of Human Evolution* 18: 329–344.

Speth, John D. 1991. Protein selection and avoidance strategies of contemporary and ancestral foragers: unresolved issues. *Philosophical Transactions of the Royal Society of London B* 334, 265–270.

Speth, John D. and K. A. Spielman. 1983. Energy source, protein metabolism, and hunter-gatherer subsistence strategies. *Journal of Anthropological Archaeology* 2: 1–31.

Srivastava, Arun and Robin I.M. Dunbar. 1996. The mating system of Hanuman langurs—a problem in optimal foraging. *Behavioral Ecology and Sociobiology* 39: 219–226.

Steegmann, Jr., A.T., F.J. Cerny, and Trenton W. Holliday. 2002. Neandertal cold adaptation: physiological and energetic factors. *American Journal of Human Biology* 14: 566–583.

Strassmann, Beverly I. 1992. The function of menstrual taboos among the Dogon. Defence against cuckoldry. *Human Nature* 3: 89–131.

Strassmann, Beverly I. 1996. Menstrual hut visits by Dogon women: a hormonal test distinguishes deceit from honest signaling. *Behavioral Ecology* 7: 304–315.

Strassmann, Beverly I. 1997. The biology of menstruation in *Homo sapiens*: total lifetime menses, fecundity, and nonsynchrony in a natural-fertility population. *Current Anthropology* 38: 123–129.

Strassmann, Beverly I., Nikhil T. Kurupati, Brendan F. Hug, Erin E. Burke, Brenda W. Gillespie, Tatiana M. Karafet, and Michael F. Hammer. 2012. Religion as means to assure paternity. *Proceedings of the National Academy of Sciences USA* 109: 9781–9785.

Stringer, Chris. 2011. *The Origin of our Species*. London: Allen Lane.

Stringer, Chris. 2012. The status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology* 21: 101–107.

Svoboda, J., V. Lozek, and E. Vlcek. 1996. *Hunters between East and West: the Paleolithic of Moravia*. New York: Plenum Press.

Szabo, B., C. McKinney, T. Dalbey, and K. Paddayya. 1990. On the age of the Acheulian culture of the Hunsgi-Baichbal Valleys, Peninsular India. *Bulletin of the Deccan College Postgraduate Research Institute* 50: 317–321.

Thomas, Elizabeth M. 1959. *The harmless people.* London: Secker and Warburg.

Tomasello, Michael. 1999. *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.

Tomasello, Michael, A.C. Kruger and H.H. Ratner. 1993. Cultural learning. *Behavioral and Brain Sciences* 16: 495-552.

Trinkaus, Erik. 1989. Neanderthal upper limb morphology and manipulation. In *Hominidate: Actes du 2eme Congres International de Paleontologie Humaine*, G. Giacobin (ed.), pp. 331–338. Turin: Jaca Book.

Trinkaus, Erik. 2004. Eyasi 1 and the Suprainiac Fossa. *American Journal of Physical Anthropology* 124: 28–32.

Trivers, Robert L. 1985. *Social Evolution*. Menlo Park, CA: Benjamin/Cummings.

Turke, Paul W. 1984. Effects of ovulatory concealment and synchrony on protohominid mating systems and parental roles. *Ethology and Sociobiology* 5: 33–44.

Turnbull, Colin M. 1984 [1961]. *The Forest People.* London: Triad Paladin.

Valensi, P. 2001. The elephants of Terra Amata open air site (Lower Palaeolithic, France). In *The world of elephants – first international congress, January 16–20, Rome 2001*, G. Cavaretta, P. Gioia, M. Mussi, and M. Palumbo (eds.), pp. 260–264. Rome: Consiglio Nazionale della Ricerche.

Vandermeersch, B. 1970. Une sépulture moustérienne avec offrandes découverte dans la grotte de Qafzeh. *Comptes Rendus de l'Académie des Sciences* 270: 298–301.

van Gulik, Robert H. 1974. *Sexual life in ancient China. A preliminary survey of Chinese sex and society from Ca. 1500 BC till 1644 AD*. Brill Archive.

Vanhaeren, Marian, Francesco d'Errico, Chris Stringer, S.L. James, J.A. Todd, and H.K. Mienis. 2006. Middle Paleolithic shell beads in Israel and Algeria. *Science* 312: 1785–1788.

van Peer, Philip, Veerle Rots, and J.-M. Vroomans. 2004. A story of colourful diggers and grinders: the Sangoan and Lupemban at site 8-B-11 at Sai Island, Northern Sudan. *Before Farming* 3: 1–28.

van Schaik, Carel P., Nancy Barrickman, Meredith L. Bastian, Elissa B. Krakauer, and Maria A. van Noordwijk. 2006. Primate life histories and the role of brains. In *The Evolution of Human Life History*, Kristen Hawkes and Richard R. Paine (eds.), pp. 127–154. Santa Fe and Oxford: School of American Research/James Currey.

van Schaik Carel P. and Michael Heistermann. 1994. Predation risk and the number of adult males in a primate group: a comparative test. *Behavioral Ecology and Sociobiology*. 35: 261–272.

van Schaik, Carel P., J. Keith Hodges, and Charles L. Nunn. 2000. Paternity confusion and ovarian cycles of female primates. In *Infanticide by males and its implications,* Carel P. van Schaik and Charles H. Janson (eds.), pp. 361–387. Cambridge, UK: Cambridge University Press.

van Schaik Carel P., Maria A. van Noordwijk, and Charles L. Nunn. 1999. Sex and social evolution in primates. In *Primate Socioecology*, Phyllis C. Lee (ed.), pp. 204–240. Cambridge, UK: Cambridge University Press.

Vértes, L.1959. Churinga de Tata (Hongrie). *Bulletin de la Société Préhistorique de France* 56: 604–611.

Voland, Eckart, Athanasios Chasiotis, and Wulf Schiefenhövel (eds.). 2005. *Grandmotherhood: the evolutionary significance of the second half of life*. New Brunswick (NJ) and London: Rutgers University Press.

Volman, T. 1981. *The Middle Stone Age in the southern Cape*. PhD dissertation, University of Chicago.

Vrba, E., G. Denton, T. Partridge, and L. Buckle (eds.). 1995. *Paleoclimate and evolution, with emphasis on human origins.* New Haven: Yale University Press.

Wadley, Lyn. 1993. The Pleistocene Later Stone Age South of the Limpopo River. *Journal of World Prehistory* 7: 243–296.

Wadley, Lyn, Bonnie Wilkinson, and Marlize Lombard. 2004. Ochre in hafting in Middle Stone Age southern Africa: a practical role. *Antiquity* 78: 661–675.

Wadley, Lyn, T. Hodgskiss, and M. Grant. 2009. Implications for complex cognition from the hafting of tools with compound adhesives in the Middle Stone Age, South Africa. *Proceedings of the National Academy of Science USA* 106: 9590–9594.

Watts, Ian. 1998. *The origins of symbolic culture: The southern African Middle Stone Age and Khoisan ethnography*. PhD dissertation, University of London.

Watts, Ian. 1999. The origin of symbolic culture. In *The Evolution of Culture. An interdisciplinary view,* Robin I.M. Dunbar, Chris Knight, and Camilla Power (eds.), pp. 113–146. Edinburgh: Edinburgh University Press.

Watts, Ian. 2002. Ochre in the Middle Stone Age of southern Africa: ritualised display or hide preservative? *South Af-*

rican Archaeological Bulletin 57: 1–14.

Watts, Ian. 2009. Red ochre, body painting and language: interpreting the Blombos ochre. In *The Cradle of Language*, Rudolf Botha and Chris Knight (eds.), pp. 62–92. Oxford: Oxford University Press.

Watts, Ian. 2010. The pigments from Pinnacle Point Cave 13B, Western Cape, South Africa. *Journal of Human Evolution* 59: 392–411.

Weaver, Tim D. and Karen Steudel-Numbers. 2005. Does climate or mobility explain the differences in body proportions between neandertals and their Upper Paleolithic successors. *Evolutionary Anthropology* 14: 218–223.

Wenzel, S. 2007. Neanderthal presence and behaviour in central and northwestern Europe during MIS 5e. In *The climate of past interglacial's*, F. Sirocko, M. Claussen, M. Sánchez-Goñi, and T. Litt (eds.), pp. 173–193. Developments in Quaternary Sciences 7. Amsterdam: Elsevier.

Wernert, P. 1957. Stratigraphie paléontologique et préhistorique des sediments quaternaires d'Alsace-Achenheim. *Mémoire du service de la carte géologique de l'Alsace-Lorraine*, Université de Strasbourg.

White, Tim, B. Asfaw, D. DeGusta, H. Gilbert, G. Richards, G. Suwa, and F. Clark Howell. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 742–747.

Whiten, Andrew and David Erdal. 2012. The human sociocognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B* 367: 2119–2129. doi:10.1098/rstb.2012.0114.

Wilhelm, J.H. 1954. Die !Kung-Buschleute. *Jahrbuch des Museums für Völkerkunde zu Leipzig* 12: 91–188.

Wilkins, Jayne and Michael Chazan. 2012. Blade production ~500 thousand years ago at Kathu Pan 1, South Africa: support for a multiple origins hypothesis for early Middle Pleistocene blade technologies. *Journal of Archaeological Science* 39: 1883–1900.

Wolpoff, Milford. 1996–97. *Human Evolution*. College Custom Series. New York: McGraw-Hill.

Wood, Bernard (ed.). 2011 *Wiley-Blackwell Encyclopedia of Human Evolution.* Hoboken, NJ: Blackwell Publishing.

Wreschner, Ernst E. 1983. *Studies in prehistoric ochre technology*. PhD dissertation, Hebrew University, Jerusalem.

Wreschner, Ernst E. 1985. Evidence and interpretation of red ochre in the early prehistoric sequences. In *Hominid evolution: past, present, future*, Phillip Tobias (ed.), pp. 387–394. New York: Alan Liss.

Zahavi, Amotz and Avishag Zahavi. 1997. *The Handicap Principle*. New York and Oxford: Oxford University Press.

Ziegler, Thomas, J. Keith Hodges, and Michael Heistermann. 2000. Hormonal correlates of reproductive seasonality in wild female Hanuman langurs (*Presbytis entellus*). *American Journal of Primatology* 51: 119–134.

Zilhão, João. 2006. Neandertals and moderns mixed, and it matters. *Evolutionary Anthropology* 15: 183–195.

Zilhão, João, D. Angelucci, E. Badal-García, Francesco d'Errico, F. Daniel, L. Dayet, K. Douka, T.F.G. Higham, M.J. Martínez-Sánchez, R. Montes-Bernárdez, S. Murcia-Mascarós, C. Pérez-Sirvent, C. Roldán-García, M. Vanhaeren, V. Villaverde, R. Wood, and J. Zapata. 2010. Symbolic use of marine shells and mineral pigments by Iberian neandertals. *Proceedings of the National Academy of Sciences USA* 107: 1023–1028.