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The Raw and the Stolen

Cooking and the Ecology of Human Origins[1]

by Richard W. Wrangham, James Holland Jones, Greg Laden, David Pilbeam, and NancyLou Conklin-Brittain

Cooking is a human universal that must have had widespread effects on the nutrition, ecology, and social relationships of the species that invented it. The location and timing of its origins are unknown, but it should have left strong signals in the fossil record. We suggest that such signals are detectable at ca. 1.9 million years ago in the reduced digestive effort (e.g., smaller teeth) and increased supply of food energy (e.g., larger female body mass) of early *Homo erectus*. The adoption of cooking required delay of the consumption of food while it was accumulated and/or brought to a processing area, and accumulations of food were valuable and stealable. Dominant (e.g., larger) individuals (typically male) were therefore able to scrounge from subordinate (e.g., smaller) individuals (typically female) instead of relying on their own foraging efforts. Because female fitness is limited by access to resources (particularly energetic resources), this dynamic would have favored females able to minimize losses to theft. To do so, we suggest, females formed protective relationships with male co-defenders. Males would have varied in their ability or willingness to engage effectively in this relationship, so females would have competed for the best food guards, partly by extending their period of sexual attractiveness. This would have increased the numbers of matings per pregnancy, reducing the intensity of male intrasexual competition. Consequently, there was reduced selection for males to be relatively large. This scenario is supported by the fossil record, which indicates that the relative body size of males fell only once in hominid evolution, around the time when *H. erectus* evolved. Therefore we suggest that cooking was responsible for the evolution of the unusual human social system in which pair bonds are embedded within multifemale, multimale communities and supported by strong mutual and frequently conflicting sexual interest.

RICHARD W. WRANGHAM is Professor of Anthropology at Harvard University (Peabody Museum, 11 Divinity Ave., Cambridge, Mass. 02138, U.S.A.). Born in 1948, he was educated at Oxford University (B.A., 1970) and Cambridge University (Ph.D., 1975). His research focuses on the evolutionary ecology of chimpanzees, which he has been studying in Kibale National Park (Uganda) since 1987. He has published (with Joseph Manson) "Intergroup Aggression in Chimpanzees and Humans" (CURRENT ANTHROPOLOGY 32:369–90), (with Colin and Lauren Chapman) "Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups" (*Behavioral Ecology and Sociobiology* 32: 199–209), and (with Dale Peterson) *Demonic Males: Apes and the Origins of Human Violence* (Boston: Houghton Mifflin, 1996).

JAMES HOLLAND JONES is a graduate student in biological anthropology at Harvard University. He was born in 1967 and received his B.A. from New College in Sarasota, Fla., in 1991 and his A.M. from Harvard in 1994. His research interests focus on demography and the evolution of primate life histories, foraging theory, and the ways in which energy availability shapes life histories. He has done fieldwork on the foraging ecology of orangutans in the Gunung Palung National Park, West Kalimantan, Indonesia, and is completing a dissertation on formal models of primate life histories.

GREG LADEN is Assistant Professor of Anthropology at the University of Minnesota. Born in 1958, he was educated at the University of the State of New York Regents Colleges (B.A., 1984) and Harvard University (M.A., 1987; Ph.D., 1992). His research interests include evolutionary theory, African prehistory, and the evolution and history of hominid ecology, with a focus on foraging adaptation. He has done fieldwork with the Efe of the Ituri Forest and prehistoric and historic archaeology in North America.

DAVID PILBEAM is Henry Ford II Professor of the Social Sciences at Harvard University. Born in 1940, he was educated at Cambridge University (B.A., 1962) and Yale University (Ph.D., 1967). His research focuses on hominoid evolution, including Miocene apes and their environments. His long-term field program in the Siwaliks of Pakistan has been running continuously since 1973. His recent publications include (with S. J. Jones and R. D. Martin, eds.) *The Cambridge Encyclopedia of Human Evolution* (Cambridge: Cambridge University Press, 1992), (with M. Brunet, A. Beauvilain, Y. Coppens, E. Heintz, and A. H. E. Moutaye) "First Australopithecine 2,500 Kilometres West of the Rift Valley" (*Nature* 378:273–74), and "Genetic and Morphological Records of the Hominoidea and Hominid Origins: A Synthesis" (*Molecular Phylogenetics and Evolution* 5:155–68).

NANCYLOU CONKLIN-BRITTAIN is a postdoctoral research assistant at Harvard University. She obtained her B.S. and Ph.D. from Cornell University in animal nutrition. Her research focuses on the nutritional ecology of primates in Kibale National Park. She has published (with Richard Wrangham and Kevin Hunt) "Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance" (*International Journal of Primatology* 19:949–70, 971–97) and "Frugivorous Primate Diets in Kibale Forest, Uganda" (*Proceedings of the Nutrition Society* 56:322A).

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The pattern of hominid[2] morphological and cultural changes can be summarized as follows (Wolpoff 1998): Australopithecines show high body weight dimorphism, have small brains and large teeth, and lack flaked stone tools (Klein 1989). With early *Homo* we see the appear-

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[2] Throughout this paper, "*Homo erectus*" includes *H. ergaster*, with the earliest specimens ca. 1.9 million years old; "later *Homo*" includes living and fossil *H. sapiens*, Neanderthals, and other non-*erectus* Middle Pleistocene hominids; "early *Homo*" includes *H. habilis* s.l. or *H. habilis* s.s. plus *H. rudolfensis*; "australopithecines" includes *Ardipithecus, Australopithecus*, and *Paranthropus*; "early hominids" includes early *Homo* plus australopithecines.

ance of archaeological associations of flaked stone tools and cut-marked bones, along with increase in brain size but little if any reduction in postcanine tooth size (Klein 1989, Holloway 1983, Wood 1992). Body size dimorphism cannot be estimated because of taxonomic and cranial-postcranial associational problems. *Homo erectus* is the first hominid in which body size dimorphism and postcranial anatomy resemble those in later *Homo*, brain size is increased over the larger-brained early *Homo* (although it is not clear the extent to which this is allometric), and tooth size is markedly reduced (Walker and Leakey 1993). We argue that the development of controlled fire and the cooking of plant foods coincided with and explains this tooth reduction and that cooking changed subsequent hominid social systems in a way that is reflected in persistently reduced sexual size dimorphism.

We focus on *H. erectus*, which exhibits a suite of traits that distinguish it significantly from earlier hominid species. These include an overall increase in body size and reduced body size dimorphism, implying a substantial increase in female body size (Walker and Leakey 1993, Lorenzo et al. 1998), reduced masticatory apparatus (smaller molars and jaws and reduced prognathism compared with gracile australopithecines) (Walker and Leakey 1993; Wood 1991, 1992), more human body proportions and build, a decrease in upper body arboreal adaptations, increased commitment to bipedalism, and prolonged bouts of activity in open and arid environments (Walker and Leakey 1993, Franciscus and Trinkaus 1988), increased absolute and probably relative brain size (Walker and Leakey 1993; Holloway 1979, 1983; Kappelman 1996; Krantz 1995), occupation of a wider range of habitats (inferred from a wider range of altitude and latitude of Acheulean sites) (see Clark 1987, Clark and Kurashina 1980, Klein 1989, Asfaw et al. 1992), and range extension from Africa to Indonesia (Swisher et al. 1994).

Several hypotheses have been proposed for this evolutionary grade shift. Darwin (1871), Dart (1953), and more recent researchers (Washburn and Lancaster 1968, Milton 1987, Trivers 1971, Tappen 1995) have emphasized the role of hunting and, in particular, the characteristics of predatory behavior and/or the use of meat itself as key factors in human evolution. These ideas involve a range of hypothesized relationships between hunting and hominization, including the need to follow migratory herds, the benefits of cooperative hunting, the importance of group size in defense against the large predators of the savanna, and the large (and therefore sharable) package size of meat. Other dietary hypotheses have included a major change in the plant diet (Tanner 1987, Peters and O'Brien 1981). Nondietary hypotheses involve changes in social or cultural behaviors such as increased provisioning by males or larger social groups (Lovejoy 1981, Dunbar 1993). In addition, throughout the history of paleoanthropology researchers have discussed the importance of controlled use of fire in relation to both dietary and social hypotheses—as a means of cooking food (Pfeiffer 1971, Stahl 1984) or defense against predators, for its role in the social dynamics of residential camps, or even as the inspiration for dance, music, and language (e.g., Goudsblom 1986, 1989).

We present a new hypothesis that links changes in diet, anatomy, and behavior at the speciation event that produced *H. erectus*. While we embrace the importance of fire in cooking food (especially plant underground storage organs), we also propose that cooking of both animal and plant foods likely involved central-place foraging with delayed consumption of food, which brought otherwise dispersed plant foods into a category previously proposed for hunted animal products: packages amenable to sharing *and* vulnerable to theft by dominant individuals (cf. Winterhalder 1996). We propose that the new relationship between foraging and social competition caused by cooking (a producer-scrounger system) led to pressure on females to form protective bonds with males and that as a consequence females benefited from being more sexually attractive to males than previously. The increase in the duration of female sexual attractiveness caused a reduction in the operational sex ratio, which led to a reduction in sexual size dimorphism. At the same time, a large increase in the digestibility of plant food and therefore in energy availability allowed an increase in especially female but also male absolute body size and a decrease in the size and robustness of the masticatory apparatus. All these changes are hypothesized to have happened rapidly, that is, as a "punctuated event," on the order of 10^4–10^5 years in duration, consequent upon the adoption of cooking by a preceding early *Homo* population.

Our hypothesis has not been fully tested, but it is consistent with various lines of evidence, accounts for many of the important changes related to human origins, and suggests new hypotheses to be tested through the fossil and archaeological record. We present it, therefore, with the aim of stimulating new thinking.

Energy Availability and Cooking of Plant Foods

Cooking is a human universal. Previous writers have suggested that because cooked foods require less extensive digestion than raw plant foods, the adoption of cooking can influence the morphology of dentition and the intestine, reducing tooth size and gut size (e.g., Sussman 1987, Aiello and Wheeler 1995, Brace 1996). Here we extend this argument by proposing that (1) raw plant foods were the predominant fraction of early hominid diets and underground storage organs were particularly important; (2) plant foods remained critical to early human diets; (3) cooking of plant foods would have caused a substantial increase in digestibility and increased the range of plants that would have been edible for hominids sufficiently to leave a recognizable signal in the fossil record and perhaps the archaeological record; (4) increased meat eating (alone, i.e., without cooking) by *Homo* would have had smaller effects on nutrition than the adoption of cooking; (5) the best interpretation of the current evidence is that fire was controlled at the origin of *H. erectus*.

PLANT FOODS IN EARLY HOMINID DIETS

Australopithecines likely derived most of their food from plants. Several lines of evidence support this assertion. First, most modern human tropical and subtropical foragers eat mainly plant foods (despite a widepsread cultural fixation on hunting of game), and the living African apes (gorillas, chimpanzees, and bonobos) derive most of their food from plants. Therefore, a parsimonious argument is that the last common ancestor of chimpanzees and hominids is likely to have done the same. Second, there is very limited paleontological and/or archaeological evidence for carnivory by these early hominids (Klein 1989, Sillen 1982). Third, two derived features in australopithecines, large molar surfaces and thick enamel, together with an analysis of microwear patterns, indicate that both *Australopithecus* and *Paranthropus* maintained plant-eating adaptations, although perhaps elaborated or specialized to some degree relative to living apes (e.g., Kay and Grine 1988). Eaton (1988), for example, suggested that plant foods composed > 90% of australopithecine diets.

In line with niche theory and empirical evidence from primates, we propose that these characteristic dental features represent adaptation to fallback foods, eaten during periods of food scarcity. Fallback foods are particularly important components of the diet because they represent the kinds of food to which anatomical and foraging specializations are expected to be adapted (see Boag and Grant 1981, Schoener 1982, Robinson and Wilson 1998). Periods of food shortage would have been frequent (e.g., annual) in all hominid habitats, as they are even in rain forest (e.g., Conklin-Brittain, Wrangham, and Hunt 1998*a*, Wrangham, Conklin-Brittain, and Hunt 1998). Seasonal shortages mean that preferred foods such as fruits and seeds would not have been consistently available (Peters and O'Brien 1994), and dental and ecological considerations easily rule out the herbaceous leaves and piths that make up the fallback foods of modern African apes such as chimpanzees (Wrangham et al. 1996). In contrast, underground storage organs such as tubers, rhizomes, and corms are likely to have been important for australopithecines because of their availability and hominid dental morphology (Hatley and Kappelman 1980), and we propose that they were the major type of fallback food. This hypothesis is supported by ecological, botanical, paleontological, and anthropological considerations.

First, underground storage organs occur at higher biomass in drier sites because they store food and/or water during periods of climatic stress (Andersen 1987). In Tanzanian savanna woodland, for example, Vincent (1984) found densities of edible tubers averaging 40,000 kg per km^2, compared with only 100 kg per km^2 found by Hladik and Hladik (1990) in a rain forest of the Central African Republic. (Even at a density of 100 kg per km^2, Hladik and Hladik considered them sufficiently abundant to support a human population.) Species diversity varies similarly. Thus, surveys of the number of species with edible underground storage organs yield a total of 101 for five African savanna sites compared with 14 for four forest sites (savanna, Lee 1979, Silberbauer 1981, Vincent 1984, Ichikawa 1987, Sept 1984; forest, Hladik and Hladik 1990, Bahuchet 1990, Terashima, Ichikawa, and Sawada 1988, Terashima, Kalala, and Malasi 1992). The four major plant families represented by these species in the African sites were Asclepiadaceae, Leguminoseae, Cucurbitaceae, and Liliaceae, which together accounted for 59.4% of species eaten.

As this distribution suggests, species that eat underground storage organs are characteristic of savanna woodlands and drier habitats. Thus, although pigs (Suidae [Hatley and Kappelman 1980]) eat them, the only nonhuman mammalian taxa in Africa known to depend closely on them are mole rats (Bathyergidae and Rhizomyidae). Mole rats are associated with xeric habitats both worldwide (Andersen 1987) and in the fossil record (Nevo 1979). In modern Africa they occur throughout the sub-Saharan woodlands and savannas, but they are not found in rain forests where apes live (Nevo 1979, Jarvis et al. 1994). In contrast to the ecological separation of mole rats and African apes, fossil mole rats have been found in the same deposits as some early hominids and some Miocene apes (e.g., *Tachyoryctes* with *Ardipithecus ramidus* [WoldeGabriel et al. 1994], *Heterocephalus* with *Australopithecus afarensis* at Laetoli [Denys 1987, Leakey 1987], and Bathyergidae in Miocene fossil hominoid sites, including Rusinga and Baringo [Lavocat 1978]). The mole-rat evidence thus indicates that underground storage organs would have been abundant in Pliocene nonforested habitats inhabited by hominids.

Second, the location of underground storage organs makes them unavailable for most mammalian taxa, but where they are abundant they represent a large food source for any species that develops a method of exploiting them. The idea that australopithecines ate underground storage organs is therefore consistent with widespread habitat occupation by australopithecines, from Ethiopia to Chad and South Africa. (In fact, australopithecines may have lived at higher population densities than forest-living apes, although it is difficult to test this hypothesis using the fossil record.) Most species with edible underground storage organs occur at depths below the 10 cm or so to which baboons and geladas dig, and therefore digging sticks would presumably have been needed to exploit them (Vincent 1984). Evidence for *Paranthropus* use of digging sticks has been presented by Brain (1988) in the form of more than 60 horns and long bones showing wear consistent with the digging of vegetable food from the ground.

Third, underground storage organs are eaten extensively by African (and other tropical) hunter-gatherers, becoming a dominant food-class during periods of food scarcity (Hawkes, O'Connell, and Blurton Jones 1997, Lee 1979, Marshall 1976, Silberbauer 1981, Vincent 1984).

Savanna baboons (*Papio cynocephalus*) and geladas

(*Theropithecus gelada*), commonly eat the pea-sized corms of grasses and sedges during periods of food scarcity (Dunbar 1977, Whiten, Byrne, and Henzi 1987, Barton et al. 1992). This adaptation supports the idea that incorporation of underground storage organs into the diet as fallback foods may have enabled primates to colonize the savanna, and the restriction of their regular use to humans and Papioninae shows that this use by humans is apomorphic with respect to African apes. Because the adoption of new food types is normally associated with dental adaptation, the eating of underground storage organs in human ancestry is most likely to be correlated with the evolution of the principal apomorphic hominid molar morphology, that is, with early australopithecines.

In summary, underground storage organs can be expected to have occurred at high density even during periods of seasonal climatic stress and have had few other animals competing to eat them. Their inclusion in the diet would explain the dental adaptations of the australopithecines (large, thick grinding surfaces and robust jaws) and would have represented a sufficient novelty to account for the evolution of an ecological grade shift. They are therefore an especially viable candidate for australopithecine fallback foods.

PLANT FOODS IN EARLY HUMAN DIETS

At least one significant change is documented at > 2.5 million years ago—the first archaeological assemblages of flaked Oldowan stone tools (Semaw et al. 1997). Soon thereafter, at > 2.3 million years ago, Oldowan tools associated with comminuted bones showing possible cut marks are known (Kimbel et al. 1996). Early *Homo* dental specimens from ca. 2.5 million years ago (Suwa, White, and Howell 1996, Kimbel, Johanson, and Rak 1997, Bromage, Schrenk, and Zonneveld 1995) show no size reduction relative to *A. afarensis* (Johanson, White, and Coppens 1982; Kimbel, Johanson, and Rak 1994), and tooth size in many early *Homo* younger than 2.0 million years remains large (Wood 1991, Johanson et al. 1987). Whatever the dietary shift associated with archaeological assemblages (presumably some increase in meat intake), there was no correlated change in tooth size.

With the appearance of *H. erectus*, there are indications that "early humans were able in some manner to greatly improve their intake and uptake of energy, apparently without any decrease in dietary quality" (Milton 1987:106). Particularly strong signals are an increase in body mass (McHenry 1992, 1994), reduction in molar size and enamel thickness (Wood 1981, Isaac 1983), and increase in brain volume (Holloway 1979, Milton 1987, Leonard and Robertson 1994, Aiello and Wheeler 1995, Kappelman 1996). Comparative data on primate energetics suggest that total daily energy expenditure rose from australopithecines to *H. erectus* by a factor of at least 40–45% and probably (assuming a human-style foraging strategy in *H. erectus*) by 80–85% (Leonard and Robertson 1997).

The predominant hypothesis for the significant dietary change has been an increase in meat intake. We propose that whatever the changes in meat intake, plants would have remained critical, especially during times of resource stress. Among tropical African hunter-gatherers, plant items always compose the majority of the diet (Hayden 1981, Hill 1982, Keeley 1988) and are vital during periods of food stress (Lee 1968, Silberbauer 1981, Bailey 1991). When plant food is scarce, hunters are probably less willing to risk energy and time in a failed search for meat. In addition, wild meat is a low-fat food which may have low nutritional quality during lean periods (Speth and Spielman 1983, Speth 1989). We therefore suggest that early humans, including *H. erectus*, continued to rely on plant foods most of the time and especially during the periods of food shortage in which natural selection would have been intense.

EFFECTS OF COOKING ON PLANT-FOOD DIGESTIBILITY

Cooking makes food more available and digestible by (1) cracking open or otherwise destroying physical barriers such as thick skins or husks, (2) bursting cells, thereby making cell contents more easily available for digestion or absorption, (3) modifying the three-dimensional structure of molecules such as proteins and starches into forms more accessible for digestion by enzymatic degradation, (4) reducing the chemical structure of indigestible molecules into smaller forms that can be fermented more rapidly and completely, and (5) denaturing toxins or digestion-reducing compounds (Stahl 1984). In its own way each of these mechanisms makes food more available, either rendering it palatable or increasing its digestibility (defined as the proportion of dry-matter intake not present in the feces).

The combined importance of these mechanisms can be categorized broadly as enlarging the diet and improving its quality. Both of these benefits are relevant for the use of underground storage organs. First, these organs are often chemically protected, apparently as a result of coevolution with mammalian herbivores (Lovegrove and Jarvis 1986). In our survey of underground storage organs eaten by African foragers, 21 (43.8%) of the 48 edible species identified required cooking to become palatable. This suggests that cooking can substantially broaden the range of edible species. Furthermore, underground storage organs are frequently considered to be improved by roasting (e.g., Silberbauer 1981). This may be partly a matter of macronutrient availability. For instance, Ayankunbi, Keshinro, and Egele (1991) found that three modes of preparing cooked cassava led to a mean increase in gross energy available of 76.1% over the value for raw cassava (306 kcal/g compared with 174.0 kcal/g). Potato starch, the principal source of digestible energy in potatoes, is highly resistant to amylase (the enzyme primarily responsible for converting complex carbohydrates into usable energy) when raw but rapidly digestible when cooked (Kingman and Englyst 1994). Similarly, the apparent digestibility of soybeans was found to increase linearly with duration of cooking, partly because of the reduction of trypsin-inhibitor activity and the proportion of tannins (Kaankuka, Balogun, and Tegbe 1996). Underground storage organs frequently contain both nonstarch polysaccharides and starch, which occurs in a variety of forms, some of them slowly digestible and resistant (Periago, Ros, and Casas 1997). In a comparison of starchy foods, Trout, Behall, and Osilesi (1993) found that the method of preparation was a more important influence on the glycemic index (a measure of the speed of digestion) than the chemical composition of the raw food, although the type of starch and starch granule was also critical. The consistent finding in such studies is that cooking increases digestibility markedly, up to 100% or more.

In view of its substantial effect on the availability and digestibility of critical food items, we can expect the adoption of cooking to have been rapid. Increased digestibility of ingested food is expected to have left a variety of signals directly or indirectly in the fossil record, including smaller teeth (partly because total chewing time would have been enormously reduced, e.g., from 50% to 10% of the day), by inference smaller guts (since food spends less time in the gut to be digested), higher body mass in females (e.g., Altmann et al. 1993) and possibly in males, depending on the nature of sexual selection, and an increase in the size of relatively expensive organs (such as brains). On this basis, there appear to be three principal candidates for the time when cooking was adopted.

First is around 2.5 million years ago, a time perhaps suggested by the first changes in archaeological assemblages and possibly increased brain size (although the first fossil evidence for increased brain size is at 1.9 million years ago [Holloway 1983]). However, there is no evidence for tooth size reduction in the early *Homo* material associated with Oldowan assemblages between 2.5 and 1.5 million years ago, and therefore we remain skeptical that this period is likely to have seen the origin of cooking.

Second is the time of the origin of *H. erectus*. The increase in overall and, particularly, female body mass coincided with a striking reduction in molar size and enamel thickness (which continues at varying rates to the present), an increase in brain size, and a decrease in gut size (deduced from the reconstructed shape of the torso, which is less apelike and more human-like than in early hominids [Walker and Leakey 1993, Aiello and Wheeler 1995]).

Third is the time, around 200,000 years ago, when early modern humans first extended their occupation of Europe from relatively mild habitats (Dennell and Roebroeks 1996) into periglacial zones. Brace (1996) has argued that these populations would have depended on cooking to thaw meat, and he proposed that cooking began with them. His hypothesis is supported by substantial evidence of cooking from burned bone and hearths, the use of "earth ovens," and the first significant reduction in tooth size since the origin of *H. erectus*. We suggest that these points favor an important increase in reliance on cooking. However, if cooking was not adopted until 200,000 years ago, much evidence of earlier uses of fire, both in Africa (see below) and in Europe (see James 1989 for review), must be discarded.

MEAT EATING IN EARLY HUMAN DIETS

There is a clear difference between apes and humans in the amount of meat eaten. If australopithecines ate as much meat as some populations of chimpanzees do, their consumption could have been 450–600 kg per 50-individual community per year (Wrangham and Bergmann-Riss 1990, Stanford 1996), about 10% of the amount eaten even by African hunter-gatherers who consume relatively little (e.g., 4,000 kg per 50-individual community per year [Tanaka 1976]). Another possible signal of increased energy availability, following Hawkes (1991), is that increased hunting *requires* efficiency in other forms of foraging, with the result that evidence for intensified hunting suggests that hominids were able to adopt this high-risk, high-gain foraging strategy. By this argument, meat is not an important source of food but, rather, hunting itself is an important behavior, less efficient than foraging for plants and thus possible only if supported by gains in efficiency in other areas of foraging. It is accordingly reasonable to think that *H. erectus* began to eat substantially more meat than earlier hominids.

Attributing the signals of increased energy availability for *H. erectus* to increased meat intake rather than to cooking has several problems. First, because of its low energy value during periods of climatic stress, meat appears unlikely to have been a fallback food (Speth 1989). Its adaptive significance would therefore be as a food type superior to those eaten during periods of food abundance, when selection has reduced effects because populations are less stressed. Second, nonhuman examples do little to support the idea that additional meat in the diet has major effects on energy availability. For example, a highly carnivorous population of chimpanzees (at Gombe) also has the smallest known body weight among chimpanzees (Stanford et al. 1994, Uehara and Nishida 1987), and polar bears, which are much more carnivorous than brown bears, have only 7% more female body mass (which itself may be less than expected simply because of latitudinal differences between the two taxa) and smaller neonates (Oftedal and Gittleman 1989). Third, for ecological reasons human meat intake would presumably have varied in importance over evolutionary time, just as it does among living populations. For these reasons, the fossil signals left by an increase in meat intake are expected to be weaker, less immediate, and more reversible than those left by the adoption of cooking. Fourth, we have tried to compare the amount of energy gained by adding meat to a prehuman plant diet versus maintaining the same plant items in the diet and cooking them. Our (necessarily crude) estimates suggest that cooking raises energy intake substantially more than substituting meat for plant items (tables 1 and 2).

Accordingly, we conclude that while the signals of increased energy expenditure at the origin of *H. erectus* were strongly linked to the adoption of cooking, the contribution to energy intake from increased meat intake is

TABLE 1
Average Percentages of Energy in Wild Foods Available to a Hominoid from Carbohydrate, Protein, and Lipid

Food Type	Carbohydrate	Protein	Lipid	Calories/g
Fruit	50	10	5	2.85
Seeds	20	15	8	2.12
USOs	30	8	4	1.88
Meat	0	60	4	2.76

NOTE: Carbohydrate, protein, and lipid values are given by Conklin-Brittain, Wrangham, and Smith (1998*b*) for plant items and Leung, Busson, and Jardin (1968) for meat. Energy values are calculated assuming 4 cal/g for carbohydrate and protein and 9 cal/g for lipid (RDA 1980).

less certain. We suggest that the presumed increase of meat consumption in later hominids was a dietary adaptation related to cooking plant material. Specifically, the increased energy availability allowed by cooking plant materials played a permissive role in the intensification of hunting—a high-risk, high-gain activity—much the way periods of fruit abundance seem to allow intensification of chimpanzee hunting (Wrangham and Bergmann-Riss 1990, Stanford 1996).

THE CONTROL OF FIRE

The potential importance of fire in human evolution has been much discussed (e.g., Hough 1916, 1932; Black 1931; Oakley and Golson 1956; Oakley 1956, 1964, 1970; Pfeiffer 1971; Clark and Harris 1985; Barbetti 1986; James 1989; Bellomo 1991). The archaeological data are confusing, because some of the most widely accepted evidence of early use of fire, by Asian *H. erectus*, is now in doubt (at Zhoukoudian [Black 1931; see Binford and Ho 1985, Binford and Stone 1986, Weiner et al. 1998]). However, more recent data from reddened areas at Chesowanja (Harris and Gowlett 1980) and Koobi Fora (Harris 1978) indicate the control of fire by African *H. erectus*. Thermal and paleomagnetic data suggest that the reddened patches at Koobi Fora (from around 1.6 million years ago) represent repeatedly used hearths (Bellomo 1994). At Swartkrans, burned bones are associated with hominid artifacts at around this time as well (Brain 1993). This suggests that the control of fire arose with *H. erectus*.

The African climate became increasingly dry in the lower Pliocene (Brain 1981*a*; Vrba 1985, 1988, 1995). Natural fires would therefore have occurred with increasing frequency. Lightning strikes, as well as volcanic activity, spontaneous combustion, and percussion sparks from rockfalls, have been identified as likely sources of fire (Clark and Harris 1985, Bellomo 1991). Bellomo (1994) notes that the 1.6-million-year-old evidence of controlled fire includes no evidence of cooking and therefore argues that fire was at first used only for heat, light, and protection against predators. Whether or not they were controlled, however, fires could have cooked plant or animal foods without hominid effort, providing an easy entrée for the use of cooking technology. Once hominids had detected the merits of cooking, we suggest, the idea would have spread rapidly.

Sexual Dimorphism and the Mating System

Among primates the fact that females are continuously sexually attractive and (to the appropriate male) near-continuously sexually receptive is a uniquely human trait. We suggest that, like cooking, the extension of female sexual receptivity should have left a strong signal in the fossil record. We begin by arguing that the signal for recognizing prolonged female sexual receptivity is a reduction in sexual dimorphism in body mass. We then ask when in hominid evolution reductions in sexual dimorphism of the appropriate magnitude can be seen.

FEMALE MATING RECEPTIVITY AND SEXUAL DIMORPHISM IN BODY MASS

In eight well-sampled modern populations, human sexual dimorphism in body mass averages 1.15 (range 1.06 [Western Samoa] to 1.24 [Japan], male divided by female) (Smith and Jungers 1997). This is an intermediate value compared with those for other primates, but when body mass is taken into account it is markedly less than expected because among primates there is a strong correlation between female body mass and dimorphism (Martin, Willner, and Dettling 1994). Median human female body mass is 53.05 kg for the samples reported by Smith and Jungers (1997). On the basis of Martin et al.'s (1994) regression data for 145 primates, a species with females weighing 53.05 kg is expected to have a male body mass of 94.80 kg, and if humans followed the primate trend, sexual dimorphism would be 94.80/53.05 or 1.79. No human population is known to have approached this figure. The positive correlation between body mass and sexual dimorphism in body mass, or Rensch's rule, has not been convincingly explained, and in fact Leigh (1992) questions its general validity. However, deviations from it are relatively well understood in terms of sexual selection theory. Relatively large male bodies are expected to represent male investment in fighting ability, and this investment is expected to increase as the number of mating opportunities decreases (Trivers 1972).

Until recently, tests of the hypothesis that competition for mates produces sexual size dimorphism used adult sex ratio within groups as the independent variable. However, adult sex ratio correlates rather poorly with primate sexual size dimorphism (e.g., Clutton-Brock, Harvey, and Rudder 1977, Alexander et al. 1979), and adult sex ratio is generally considered a poor proxy for the intensity of intrasexual competition (Kvaremo and Ahnesjö 1996). In their attempt to solve this problem, Mitani, Gros-Louis, and Richards (1996) noted that the intensity of male-male competition should vary not only

TABLE 2
Effects on Daily Energy Intake of a Hypothetical Early Homo *Diet of Adding Different Proportions of Meat versus Cooking*

	Early *Homo* Diet			20% Meat		40% Meat		60% Meat		Cooking, No Meat	
Food Type	% of Diet	Cal/day	g/d	g/d	Cal/day	g/d	Cal/day	g/d	Cal/day	g/d	Cal/day
Fruit	20	400	140	112	320	84	240	56	160	140	400
Seeds	20	400	189	151	320	113	240	75	160	189	491
USOs	60	1,200	638	511	960	383	720	255	480	638	1,966
Meat	0	0	0	194	534	387	1,067	580	1,601	0	0
Total	100	2,000	967	967	2,134	967	2,267	967	2,401	979	2,857
Percent change					6.7		13.4		20.0		42.9

NOTE: A 2,000 cal/day diet composed of 20% fruit, 20% seeds, and 60% underground storage organs is assumed for early *Homo*. The total dry matter of food this diet would imply (967 g) was calculated from data in table 1, and for all subsequent calculations total dry-matter intake was held constant. Including meat in the diet was assumed to reduce intake of all other food items equally. Cooking was assumed to double the energy value from carbohydrate in underground storage organs and increase it by 60% in seeds.

with sex ratio but also with the number and length of female mating cycles, which will determine what proportion of the time a given female is potentially sexually receptive. Therefore, they defined the operational sex ratio (OSR), a measure of the number of males effectively competing for each available female, as $(M/F) * (B/C)$, where M and F are the numbers of adult males and females, B is the duration of the interbirth interval, and C is the number of female mating days between births. Using this index and appropriate methods for controlling for phylogenetic correlation, they found that deviations from Rensch's rule among 16 species of apes and monkeys were well explained ($r^2 = 0.49$).

Because they included *Pan*, *Gorilla*, and *Pongo* but not *Homo*, we repeated their analysis including human data from two natural-fertility hunter-gatherer populations: the !Kung of Botswana (Howell 1979) and the Ache of eastern Paraguay (Hill and Hurtado 1996). Using a conservative estimate of the duration of postpartum sexual abstinence (one year), we calculated a value for the human OSR of 1.65, considerably lower than for any other species in the Mitani et al. sample. To evaluate the relationship between sexual size dimorphism and OSR, we used Felsenstein's (1985) test for correlated evolution of continuous characters. The bivariate relationship was estimated using model I linear least-squares regression. Data points used in the regression, known as independent contrasts, represent changes in a trait's value at or following a speciation event from the common ancestor of two extant taxa. Including humans in the analysis produced no qualitative changes in the model ($r^2 = 0.41$, $p < 0.005$, d.f. = 1, 16).

The results of our analysis mean that, in line with the primate data, low sexual dimorphism in humans is attributable to our low OSR. Whereas some components of human OSR, such as the breeding sex ratio and interbirth interval, deviate little from those of other primates, the number of mating days between births is exceptionally high. For example, human communities have somewhat similar adult sex ratios to that of chimpanzees (M/F ~ 1) and an interbirth interval in a similar range (3–7 years) (Galdikas and Wood 1990), but humans' total number of female mating days between births is as much as an order of magnitude greater. Thus for chimpanzees C was estimated by Mitani et al. (1996) as 73.5 (12.5 mating days per month, 5.9 mating cycles per birth), but for humans it can be estimated as several hundred. Postpartum sexual relations in natural-fertility human populations typically resume long before women are fully fecund. For example, Hill and Hurtado (1996) report that the Ache try (with limited success) to abstain from sexual intercourse for a year following the birth of a child. Given that the average interbirth interval was 37 months (Hill and Hurtado 1996) and that intercourse continues several months into pregnancy, this means that the Ache have 19 or more receptive cycles per pregnancy (C = 19 cycles × 25 receptive days/cycle = 475 days). Because the Ache are a particularly high-fertility group (TFR ~ 8), this value for C may be a lower bound; using !Kung data (TFR ~ 4.5) the value of C is 725. These estimates suggest that the low degree of human sexual dimorphism is influenced more closely by the high number of female mating cycles than by other components of OSR.

The nonhuman primate that most closely approaches humans in number of mating days between births is the bonobo (*Pan paniscus*). Bonobos resume mating after birth earlier than chimpanzees (about a year), continuing for about two weeks per month for the next two years or more (Kano 1992, Stanford 1998). This gives them a lower OSR than chimpanzees. Following Mitani, Gros-Louis, and Richards (1996), therefore, they would be expected to have less sexual dimorphism in body mass than chimpanzees. Sexual dimorphism in body mass is in fact marginally higher in bonobos (Jungers and Susman 1984), but they do show reduced sexual dimorphism in brain size (Cramer 1977), cranial dimensions (Cramer 1977), the permanent dentition (Kinzey 1984), and postcranial morphology (Jungers and Susman 1984, Zihlman and Cramer 1978). This inconsistency remains to be explained. Ecological influences on growth rate appear to be a promising avenue (Leigh and Shea 1996).

SEXUAL DIMORPHISM IN BODY MASS IN HOMINID EVOLUTION

The functional significance of hominid sexual size dimorphism is not well understood (Plavcan and van Schaik 1997). However, previous analyses have not considered the evolution of low OSR. If human evolution followed the nonhuman primate pattern, the time when the number of female mating cycles increased to the modern human pattern should be recognizable in the fossil record by a marked decline in sexual dimorphism in body mass.

Body weights for fossil hominids are notoriously difficult to estimate, as is dimorphism, given problems in sexing specimens. Given the range of problems associated with regression-based estimates (see Smith 1996), we have followed Smith's advice and used, wherever possible, studies that depend directly upon measurements rather than inferred body weights. We assume here that the best australopithecine estimates are for *A. afarensis* and show that this species was considerably more dimorphic than *Pan* and perhaps as dimorphic as *Gorilla* or *Pongo*, that is, with a male/female body weight ratio of as much as 2 (Lockwood et al. 1996, Richmond and Jungers 1995). Using a morphometric approach, Ruff and Walker (1993) infer a body mass for a female *A. afarensis* (AL 288-1, "Lucy") of 23.5 kg, implying male body weights averaging around 50 kg. Other australopithecine species estimates are, in our opinion, less reliable, but all estimates suggest that australopithecines as a group were markedly more dimorphic than humans.

Early *Homo* estimates of dimorphism and how it is patterned are complicated by several factors: the number of species represented in the sample, the fragmentary nature of much of the material, problems of identification of isolated postcranial material, and the lack of association of cranial and postcranial material (Wood 1985). Some individuals (OH 62, for example) were clearly very small and similar in weight to the *A. afarensis* specimen AL 288-1 (Johanson et al. 1987). Other early *Homo* postcranial material from Olduvai (Day 1977) is also markedly smaller than *H. erectus* or later *Homo*. Of the morphologically more derived early *Homo* postcranial specimens, the femora KNM-ER 1472, 1481, and 3728 have body weights estimated at 45–47 kg (Ruff and Walker 1993), while the innominate S228 is recorded as falling dimensionally "within the upper part of the size range of modern human male hip bones" (Rose 1984). If all the early *Homo* postcranials represent a single species, it is highly dimorphic, no larger than *A. afarensis* but morphologically very (too?) diverse. Also, the long-assumed association of ER 1472, 1481, 3728, and 3228 with early *Homo* is now rendered dubious because of the apparent overlap in time with what appears to be a very early *H. erectus* cranial fragment, ER 2598 (Wood 1991:130). In our view the best that can be said about the early *Homo* postcranial material is that there is currently no evidence that the amount and patterning of dimorphism are like that of either *H. erectus* or later *Homo*.

With *H. erectus* the material is somewhat better. Using the small samples from the Early Pleistocene of Kenya and the Middle Pleistocene of Zhoukoudian, China, body weight dimorphism in this species is not markedly different from that in living humans (Ruff and Walker 1993). All estimates fall within the 50–60 kg range, and the ratio of a male (WT 15000) of 68 kg and a probable female (ER 1808) of 59 kg (1.15) matches that for living humans. Estimates of dimorphism in a Middle Pleistocene later *Homo* sample from Spain, using postcranial measurements rather than weight estimates, also shows no difference in dimorphism from living humans (Arsuaga et al. 1997). Dimorphism estimates for Neanderthals, again using direct postcranial measurements, show little difference from living humans (Trinkaus 1980). Using estimates of stature, there are no differences between European Upper Paleolithic samples and living European populations (Frayer 1980), while morphometric body weight estimates for two European Upper Paleolithic males and one female from Předmostí yield a ratio of 1.18, within the range for human populations (Ruff 1994).

In summary, the modern human pattern of low sexual dimorphism occurs first with *H. erectus* and is then maintained. These data suggest that the modern human pattern of extended female sexual receptivity was initiated at the same time as cooking. Whether ovulation became concealed and females became more attractive to males at the same time as female sexual receptivity was extended is uncertain, since there are no fossil signals of these features. However, it appears most parsimonious to think that these three features developed together (e.g., Strassman 1981, Turke 1984).

Social Bonding and the Division of Labor: The Theft Hypothesis

The origins of female-male bonding in humans are not yet understood but have been addressed in terms of two major sets of ideas. Male-provisioning hypotheses suggest that bonds were based on the benefits that mothers obtained by being provisioned by males, especially with meat (e.g., Alexander and Noonan 1979, Lovejoy 1981). Bodyguard explanations, on the other hand, suggest that the important function of sexual bonds was to protect females from male violence (Smuts 1992, Mesnick 1997). Our proposal is that females formed bonds with males to protect themselves from food thieves, with the result that to a large extent females provisioned males. Pressure on females to form effective bonds then selected for extended and intensified female sexual attractiveness.

BONDS AS A PROTECTION AGAINST THEFT

Food becomes more vulnerable to theft when it is cooked. It is collected from a potentially broad area and concentrated in a small one where it remains visible and temporarily stationary but accessible and movable. Patch size is large compared with that of food being collected for immediate eating, since it represents the output of many minutes or hours of foraging effort. Furthermore, food rises in value while being cooked, because the closer it is to being ready for eating, the less investment is required to prepare it. All this means that cooked meals are more valuable than naturally occurring food items and therefore competition for them is more worthwhile. In particular, dominants who are able to steal from subordinates could in theory feed themselves simply by waiting until food was cooked and then taking over the cooking site.

The opportunity created by cooking for food theft is an example of a producer-scrounger game (Barnard 1984), a game in which individuals can exploit the efforts of others who create food patches or enhance food-patch value. In bird flocks, for example, some individuals (producers) may search for food patches while others (scroungers or parasites) merely wait until producers start feeding and then quickly join them. Among primates, savanna baboons and geladas play producer-scrounger games when eating buried corms. Subordinate individuals may be driven from a corm patch after their digging has enhanced the patch value by reducing the residual time to obtain the corms. Enhanced patch value means that theft pays.

The theory of producer-scrounger games is not highly developed, but some of the elements are clear. Where dominant-subordinate asymmetry is pronounced (Barta and Giraldeau 1998), dominant individuals are expected to scrounge more and subordinates to produce more. Early hominid males, being significantly larger than females, are likely to have been socially dominant to them, particularly if male philopatry, female transfer, and male-male coalitions were present and female-female coalitions absent (Wrangham 1987, Di Fiore and Rendall 1994). We can expect that males scrounged from females, who produced. Shortly after the adoption of cooking, therefore, the threat and/or practice of male theft would have led to cooking's becoming primarily a female activity.

This means that females would have benefited by protecting themselves from male theft. In a variety of animals, including humans, alliances between females and males serve to protect females from male sexual coercion (Hooks and Green 1993, Smuts and Smuts 1993, Mesnick 1997, Palombit, Seyfarth, and Cheney 1997, van Schaik and Kappeler 1997). Among humans, those who view female-male bonds as protective consider the male bodyguard role to be principally against male sexual aggression. Food theft could be considered a form of sexual coercion (*sensu* Smuts and Smuts 1993), because if female reproduction is energy-limited males who steal female-gathered resources are exploiting females in a reproductive domain. However, sexual coercion is normally considered in terms of aggression over mating access. For at least two reasons, food theft appears a viable alternative explanation of protective bonds. First, it explains aspects of the division of labor in foraging societies that are otherwise not easily understood (Tooby and DeVore 1987). Why do women gather? They are forced to do so because they won't acquire food otherwise and access to resources is critical for their reproductive success. Why don't men gather (much)? They don't need to because they can scrounge plant foods from women. Why do men hunt? They can afford a high-risk, high-gain activity because they are supported by women's foraging and food preparation effort.

Second, although the theft hypothesis specifies why it pays males to be aggressive, the sexual-coercion (bodyguard) hypothesis faces the problem that if females are willing to mate there is no need for coercion. Among some other primates, such as bonobos females are so willing to copulate that sexual coercion is essentially absent (Kano 1992). In such species, it is generally assumed that multiple paternity has the benefit of protecting infants from infanticide (Hrdy 1981, Wrangham 1993). The sexual-coercion hypothesis therefore needs an explanation for the unwillingness of hominid females to mate with any male who shows sexual interest. The theft hypothesis provides such an explanation in terms of female agency, since we envisage that females would achieve the most satisfactory bodyguard relationships by attracting certain males and refusing others.

The theft hypothesis suggests that females protected their resources by forming alliances with males. An alternative possibility is that females formed protective alliances with each other, as occurs in bonobos and a variety of female-bonded primates (Smuts and Smuts 1993). For several reasons, we consider this scenario less likely. First, female-female alliances in other primates rarely involve protecting resources from males. They may be unstable when resources are the object of competition, because disputes may arise within the alliance over the apportionment of resources. Male motivation to steal will also be high, because a male who has expected to eat but failed to steal from a pair of females will face a high opportunity cost (several hours of foraging). Additional considerations are the scarcity of evidence among modern humans of female-female alliances to protect resources against males, whereas marriage is essentially universal, and the observation that among foragers females sometimes forage alone during periods of food scarcity (Silberbauer 1981). Female-female alliances thus appear improbable, but they are theoretically possible. Appropriate models are required for understanding the circumstances in which they would be favored.

INTERSEXUAL BONDS AND FEMALE SEXUAL ATTRACTIVENESS

Whatever their differences, the bodyguard and theft hypotheses agree in proposing that male aggression creates a pressure among females for protective alliances with individual males. What, then, determines the relative leverage of dominants and subordinates? The dominant's power is in theory constrained by the subordinate's options outside the group: the more options available to the subordinate and the fewer available to the dominant, the less the dominant's power (Vehrencamp 1984).

In the context of hominid food theft, dominants enter the relationship with a strong power advantage. We propose that females benefited by constraining males through increasing their own sexual attractiveness. Thus, we suppose that pre-cooking hominids had a mating system in which females had few, relatively brief cycles for every birth, as occurs in most primates. A female vulnerable to food theft would have benefited by bonding with as physically or socially dominant a male as possible. Although more than one female could have bonded with a particular male and vice versa, competition would still have arisen among females for bonds with the best males. Males would have benefited by using their protective power to obtain as many fertile matings as possible and to inhibit matings by other males. Males' interest in exploiting their power to gain matings would therefore have been balanced by females' interest in retaining males' interest in their own protective bonds.

Out of this dynamic, we propose that females who could sexually attract particular dominant males more often (through exploitation of preexisting male biases [Ryan 1997]) would have been better protected against theft. Competition would therefore have ensued among females in which females became increasingly sexually attractive over increasingly long periods to exploit male interest in investing in their protection. It is this "arms race" resulting from cooking that we see as responsible for the extension of female sexual receptivity to the almost continuous pattern of modern humans. In view of the inverse relationship between female sexual receptivity and sexual dimorphism in body mass, therefore, reduced sexual dimorphism is expected to have evolved in response to cooking. Evidence reviewed above suggests that it did so.

It is striking that among all modern humans, women tend to be the cooks (Goody 1982). Indeed, cooking was more strongly associated with gender than any other variable considered in Whyte's (1978) cross-cultural survey of the status of women. The theft hypothesis easily accommodates this aspect of the division of labor, as well as others. For example, male hunting can be viewed as facilitated by the risk-minimizing productivity of female cooking, and male provisioning of females (and offspring) is explicable as in other models, by parental investment or mate acquisition (e.g., Hawkes 1991, Hawkes, O'Connell, and Blurton Jones 1991, Hill and Kaplan 1993, Hill and Hurtado 1996).

Discussion

Lévi-Strauss (1969) proposed that humanity began with cooking. We agree, because according to current evidence the timing of changes in female body size, tooth size, gut size, brain size, and sexual dimorphism in body mass appears to us strongly supportive of a connection between cooking and hominization. Strictly speaking, however, our theft hypothesis in the narrowest sense is noncommittal about the relationship between cooking and human origins. Instead, the critical logic is that cooking, whenever it evolved, led rapidly to the evolution of males' scrounging from females and thence to sexual alliances. Thus, although we think Brace's (1996) hypothesis for a late origin of cooking is improbable, we would argue, if Brace is proved right, for a late origin of sexual alliances.

Our hypothesis is that sexual alliances emerged from the adoption of cooking, particularly of plant foods. Close alternatives are that the theft which precipitated the evolution of sexual alliances was not of cooked underground storage organs but of other items, such as uncooked underground storage organs or meat (before or after cooking). Although more alienable than typical plant items eaten by foraging primates, none of these items has the same potency for promoting sexual bonds as cooked underground storage organs, with their high energy yield, predictable collecting locations, and increased value as a result of cooking. It is likely that females never controlled meat and therefore it could not be stolen from them. A diet based on raw underground storage organs may also have created a need for protection, however, for baboons and geladas digging for roots appear to benefit from alliances (e.g., Whiten, Byrne, and Henzi 1987). In future it would therefore be worthwhile to consider this possibility.

Cooking would not necessarily have been obligatory. For example, it could have begun as a mainly dry-season activity, practiced particularly during periods when underground storage organs were needed as fallback foods. We propose that at the time it evolved, females were vulnerable to theft by a number of males and therefore benefited most by bonding with the most dominant individuals, either one-to-one or with limited polygyny. Males, meanwhile, would have competed for access to the most attractive females ("attractive" here implying more than merely sexual attraction, i.e., including traits such as perceived abilities in political manipulation, bonding, mothering, etc.). The implication is that the groups in which fire-controlling hominids fed (i.e., cooked their foods) were multifemale and multimale. There are many obvious advantages to group living for a terrestrial hominid, including mutual protection against predators, returning to a consistent site of fire, maintenance of intragroup aggressive alliances, and defense or aggression against neighboring groups. The adoption of fire by *H. erectus* could certainly help to explain why arboreal adaptations were no longer at a premium, why group eating (and group sleeping) would have paid, and why this species was able to expand its geographical range beyond Africa.

The adoption of fire can also explain other aspects of hominization. With respect to life history, increased protection against predators would have reduced adult mortality and therefore favored reduced senescence and longer life-span (and therefore could have added to the selection for larger adult female body size, independent of increased energetic productivity, since the value for fitness of adults relative to juveniles increased [Charnov and Schaffer 1973, Hill 1993]). Cooked foods available for infants would also have enabled mothers to shorten the period of weaning. And, as we have suggested, the predictable availability of digestible energy in the form of underground storage organs cooked by females not only would have changed female foraging strategies and activity budgets but could have promoted the development in males of high-risk, high-gain foraging strategies such as hunting or scavenging. This concept could contribute to explaining why hunting strategies are suboptimal in terms of calorific gain (Hawkes, O'Connell, and Blurton Jones 1991).

Additionally, fire and its exchange could have had other important social ramifications. A striking feature of individuals' giving each other fire is that the high benefits conferred by receiving fire come at a trivial cost to the donor. This cost/benefit asymmetry suggests that in communities dependent on fire there would have been selection for readiness to reciprocate: an interesting question is whether this readiness would have been generalized to other contexts. Communities were probably subject to intercommunity hostility (Wrangham 1987, Wrangham and Peterson 1996), which is expected to generate relatively egalitarian relationships among fighters within communities (Vehrencamp 1983). But egalitarian relationships among males are in conflict with the potential for theft of valuable items among them. To reduce the theft potential, therefore, there may have been intensified selection for psychological mechanisms that regulate competition. Respect for ownership is one such mechanism, prominent among male hamadryas baboons (*Papio hamadryas*) (Bachmann and Kummer 1980). Thus, ironically, the creation of a potential for theft may have contributed to male egalitarianism (cf. Boehm 1996). In general, effects of a producer-scrounger system are highly sensitive to frequency-dependence of phenotypes and to the value of power asymmetries, suggesting that there can be rapid evolution to new equilibria (Barta and Giraldeau 1998).

Regardless of when cooking evolved, the theft hypothesis offers an opportunity for rethinking the evolution of sexual alliances. It generates a number of relatively specific expectations about hominid anatomy that will be testable from an improved fossil record, from nutritional data on the effects of cooking and the benefits of meat eating, from an increasingly confident theory of sexual dimorphism, and by comparison with the male-provisioning and bodyguard hypotheses. It suggests tests such as searching for paleontological evidence of the eating of underground storage organs or ethnographic studies of the relationship between a woman's marital status and her ability to acquire resources. Game-theory modeling should also help to probe assumptions such as that male-female alliances are more effective than female-female alliances in protecting females from male scrounging.

By focusing on the social and sexual dynamics that flow from competition over resources, the theft hypothesis implies that human sexual bonding evolved as a way of manipulating social relationships. Females gained protection, and males gained increased sexual access (albeit less valuable in terms of fitness) and food. This leaves undecided the question of whether sexual relationships were exclusive. The evolution of prolonged female sexual attractiveness would have given females frequent opportunities to mate. But the number of males they mated with would have depended on variables such as the nature and intensity of female-female competition, the benefits to females of multiple mating, the ability of females to avoid sexual coercion, and the ability of males to mate-guard (which would itself have depended partly on linguistic ability [Rodseth et al. 1991]). Thus, the framework we have developed merely provides a starting point for understanding how sexual alliances influence the evolution of the nuclear family. If the theft hypothesis is supported, further analysis will be necessary to understand its interplay with economic cooperation between the sexes, sexual coercion, and other dynamics of the complex human bonding system.

Comments

C. LORING BRACE
Department of Anthropology, University of Michigan, Ann Arbor, Mich. 48109, U.S.A. 23 IV 99

First off, I have to express my gratitude to Richard Wrangham and his colleagues for having asked CURRENT ANTHROPOLOGY to include me among the commentators on their essay even though they were fully aware of the fact that I look upon their gambit as belonging more to the realm of anthropological folklore than to that of science. Now, what they have produced may not be science, but it has the makings of an absolutely charming story—although its implications embody a stereotype that is guaranteed to grate on feminist sensibilities, the archetypal picture of the female as defined by the role of provider of food and sexual gratification. While this story may be sufficient for anthropological mythology, there are some basic factual matters that need to be treated. For example, it is not true that australopithecines lacked flaked tools. In fact, flake tools were the only ones of which we have actual evidence that they possessed. Oldowan "pebble tools" apparently were not tools at all but the blanks from which flakes were struck; evidently those flakes were the real items used to deal with the world with which their makers were confronted (Toth 1985). It has been experimentally shown that the cut marks on ungulate long bones at Plio/Pleistocene butchering sites could only have been made by stone flakes and not by carnivore teeth (Shipman 1983, Shipman and Rose 1983). It would appear, then, that scavenging, as posited by Schaller and Lowther (1969), and especially of pachyderms with the aid of those Oldowan flakes as suggested by Brain (1981*b*), may very well have been the avenue by which pre-*Homo* hominids moved toward a greater utilization of meat in the diet and ultimately to full membership in what Alan Walker has called "the large carnivore guild" (Walker 1984:144; Brace 1995*b*:162, 169n).

From the time of the first documented appearance of cooking between 200,000 and 300,000 years ago (Straus 1989, and see Brace 1995*b*), however, dental dimensions, which had remained in stasis for the preceding million years, have undergone a reduction in each of the regionally continuing populations of the world strictly in proportion to the length of time that cooking has been a part of the food preparation techniques of the areas in question (Brace, Rosenberg, and Hunt 1987; Brace, Smith, and Hunt 1991; Brace 1995*a*, *b*, n.d.). The greatest extent of reduction from the common Late Middle Pleistocene level is among those who first applied heat to food out of sheer necessity. This is why the phenomenon has been referred to as "obligatory cooking" (Brace 1995*b*:228; 1996:92–97) and even the "culinary revolution" (Brace 1979:546; 1995*b*:228). The archaeological record clearly shows that humans had been able to occupy the temperate zone of the western half of the Old World through the last two glacial maxima and that one of the keys to their ability to survive was control of fire (Straus 1989, and see Brace 1995*b*). Not only was this necessary as compensation for the tropical physiology bequeathed us by our ultimate African heritage, but it was also mandatory in ensuring access to essential edibles. Riss or Eemian mammoth hunters could scarcely have eaten a whole pachyderm in a single meal. After the lapse of a Pleistocene winter weekend, the rest would then have become frozen solid before it could have served as the basis for another repast.

Granted, there is a real question concerning whether they actually hunted mammoths, but aurochs was definitely on the menu, and even the hungriest band of Neanderthals could scarcely have consumed an entire Pleistocene cow at a single sitting. For years I have argued that the impetus for the control of fire in the first place and its use for cooking purposes was the access to the abundant faunal resources of the northern parts of the Old World this gave an otherwise physiologically tropical hominid (Brace 1967, 1977, 1979, 1995*b*; Brace, Rosenberg, and Hunt 1987; Brace, Smith, and Hunt 1991). The control of fire, then, was the key to the permanent occupation of the temperate zone, and it dates back nearly 300,000 years. The expanded range of occupation that followed provided the diverse selective-force spectrum that is behind the variation in adaptive traits now visible in human physical form.

There is a final point not mentioned by Wrangham et al.'s treatment of the initial control of fire. The ability to understand what is involved in actually kindling and maintaining a fire and the capability of transmitting that understanding to subsequent generations almost certainly indicates the presence of language as we know it (Ronen 1998). Indeed, it is difficult to imagine how the control of fire could have been maintained and perpetuated *without* language. One of the sources cited by Wrangham et al. even goes to the extent of suggesting that "the exigencies of living *with* fire may well have contributed to the singular development of the human capacity for language and thought" (Goudsblom 1992:23; expanded from Goudsblom 1989:169). This takes it even one step beyond the quoted view of Charles Darwin, who remarked that the discovery of "the art of making fire . . . [was] . . . probably the greatest, excepting language, ever made by man" (Darwin 1871:132).

Darwin specifically mentioned the role of cooking, "by which hard and stringy roots can be rendered digestible, and poisonous roots or herbs innocuous." The latter is certainly the case, but the archaeological evidence suggests that obligatory cooking was first developed to deal with the problem of frozen meat leftovers in the northern reaches of human occupation during the late Middle Pleistocene and only later applied to the treatment of plant materials. The dramatic rise in the quantity of plant foods in the human diet toward the end of the last glaciation is clearly indicated by the change in the quantities of the trace element strontium in human bone (Schoeninger 1980, 1982). That major increase in the presence of plant foods in the human diet is also accompanied by the first appearance of silicon polish on what have been interpreted as sickle flints and of mortars and pestles of the sort used by recent peoples for pounding and grinding roots and seeds (Bar-Yosef 1998), which are not easily digested by the human gut unless they have been altered by both mechanical and thermal means. It was only after this that the vast resources of the plant world could be deliberately exploited as a major basis for human sustenance. This terminal Pleistocene focus on plant foods led directly to agriculture, and the rest, as the saying goes, is history.

The transformation of *Australopithecus* into *Homo* was accompanied by a reduction in the degree of sexual dimorphism to a proportion that is closer to the "modern" human level. At the same time, body size had approximately doubled (Ruff et al. 1993). The reduction in sexual dimorphism was indeed the result of an even greater increase in female as contrasted with male body size, but the guess that this was driven by an increase in female sexual desirability in the eyes of the male is more akin to male wishful thinking projected into the past than to anything that can be derived from an assessment of the available evidence. Brain size had undergone a quantum expansion in proportion to body size, and the time associated with growth and maturation had expanded beyond that still visible in the anthropoid apes (Smith 1990, 1992, 1993; Smith and Tompkins 1994; Smith, Crummett, and Brandt 1995). This suggests that total life span also was more on the order of that characteristic of living humans than of their closest anthropoid relatives, and it also suggests that pregnancy was approaching a nine-month duration rather than the shorter anthropoid span. The sheer mechanics of carrying a fetus for a full nine months and then giving birth to a larger-brained neonate are more likely reasons for the increase in female body size than the suggestion that males found the sexual attractiveness of a larger female sufficient reason to form a durable pair bond (Brace 1995*b*:152; Ruff 1995).

One can guess that the make-over of *Australopithecus* into *Homo* was driven by a major change in adaptive focus that accompanied the hominid entry into membership in the large-carnivore guild. The stress on increased innate intellectual capacity that accompanied the conversion of that unlikely biped into a facultative carnivore is almost certainly the reason for the increased brain size. Along with that, it is possible to suggest that early *Homo* had gained enough wit to make the association between copulation and consequent pregnancy. From that it is but a short step to male awareness of paternity. Surely the male-female pair bond owes as much to a joint perception of parenthood as it does to the continued sexual attractiveness and availability of the female partner. One could almost regard the pair bond as a kind of product of kin selection (Wimsatt 1980: 250).

At just that point where cooking becomes clearly documented in the archaeological record, we also see a cessation of the gradual cerebral expansion of the previous 2 million years. In addition, we see the appearance of minor but identifiable regional differences in the details of the fabrication of functionally identical tools. The pattern of the distribution of those stylistic differences looks startlingly like a picture of language family relationships, and it is hard to avoid the suspicion that this, along with the universal control of fire, suggests that a version of language as we know it had become a common human attainment. The claim that "the Neanderthals lacked complex spoken language because they did not need it" (Stringer and Gamble 1993:217) can only be made in the absence of a consideration of the above and could well be called a manifestation of "Neandrophobia" (Brace 1995*b*).

HENRY T. BUNN
Department of Anthropology, University of Wisconsin, Madison, Wis. 53706-1393, U.S.A. (*htbunn@facstaff.wisc.edu*). 28 V 99

Wrangham et al. offer a story of the behavioral ecology of early Pleistocene *Homo* that requires the use of digging sticks to obtain deeply buried tubers and the controlled use of fire to cook them. As an alternative to the prevalent view that the incorporation of high-quality meat into the hominid diet selected for encephalization and the evolution of more human-like behavior in early *Homo*, the cooked-tuber story will appeal to readers for whom concepts such as "meat," "hunt," and "kill" are dreaded four-letter words and unwanted elements in human ancestry. Not since *On Becoming Human* (Tanner 1981) and *Woman the Gatherer* (Dahlberg 1981) has there been such a reaction against the view that hunting, scavenging, and the acquisition and consumption of meat (including animal fat) had an influential role in the early evolution of the genus *Homo*. The social and political interest in such a story is perhaps illustrated by the fact that the copyrighted article itself was provided to a noted U.S. science journal and critiqued there in sympathetic fashion more than six months prior to its publication. Is the cooked-tuber story science, or is it half-baked wishful thinking? To address that question, I comment on the actual evidence of controlled fire and of digging sticks.

Fire happens! The evidence indicates that there was fire at the 1.64-million-year-old site of FxJj 20 at Koobi Fora, Kenya, in the form of patches of baked sediment and several discolored and fractured stone tools (Bellomo 1994). But whether the fire coincided temporally with the presence of hominids there remains very problematic. That the fire at FxJj 20 was hominid-controlled is advocated mainly by the author of the fire study itself. One problem is that at the same stratigraphic level as FxJj 20 and within a few hundred meters laterally there are dozens if not hundreds of comparable patches of baked sediment unassociated with archaeological materials. Those are dismissed by Bellomo as inconsequential. "Flecks" and "lumps" of baked sediment have been reported from the 1.42-million-year-old Chesowanja site in Kenya (Gowlett et al. 1981; Clark and Harris 1985: 13), but those are in a fluvially redeposited small stream context. Patches of baked sediment have been reported from Pliocene contexts in Ethiopia, near where *Australopithecus afarensis*, including the famous Lucy skeleton, was found (Clark and Harris 1985). With due apologies to the Beatles, "Lucy at the Campfire with Tubers" is not going to sell. Using comparable evidence to propose a similar dietary and technological adaptation in early *Homo*, including early *H. ergaster*, is not at all convincing. Yet another early site with evidence of fire is the Swartkrans cave site in South Africa, where burned bone is reported from Member 3 from approximately 1.0 million years B.P. (Brain 1993). The problem with attributing fire at Swartkrans to hominid production is that the Swartkrans material, including hominid and other animal fossils, stone tools, bone tools, and burned bone, is all in a complex, secondary context. All of it reached the cave from the open-air landscape near the entrance to the cave by falling in, flying in, washing in, and so on, over vast amounts of time. That means that the origin of the burning on the bones is unexplained. Where is the evidence or compelling logic that early *Homo* controlled or cooked with any of those plausibly natural, nonanthropogenic fires?

The evidence of digging sticks for gaining access to deeply buried tubers in the early Pleistocene is even less convincing. Wrangham et al. rely on evidence of bone tools from Members 1–3 at Swartkrans to suggest that digging sticks of the sort used by modern foragers to dig up deeply buried tubers were even within the grasp of relatively small-brained robust australopithecines there. Modern foragers commonly use stout wooden digging sticks that are several feet in length and approach a kilogram or so in weight. Tuber gathering by the Hadza, for example, requires laborious digging through rocky soil and the use of digging sticks to lever very heavy boulders out of the way. In stark contrast, the bone tools from Swartkrans are predominantly small splinters of limb shaft that are probably graspable in only one hand. Indeed, Brain et al. (1988) replicated those pieces and used the experimental replicas, which were 10–15 cm long, to scratch around in the rocky topsoil to gather lily bulbs also used by baboons, not to dig for deeply buried tubers. There is very little in common between the scratching sticks from Swartkrans and actual heavy-duty digging sticks used by modern foragers to gather deeply buried tubers.

It is widely recognized that the fossil and archaeological record is very incomplete and biased against the preservation of organic remains, particularly plant remains and organic evidence of controlled fire. We may be seeing just the tip of the iceberg in the actual surviving evidence from the early Pleistocene. As a consequence, the behavioral capabilities and adaptations of early *Homo* may be seriously underestimated. From that perspective, the authors of the cooked-tuber story may be exactly right. Early *H. ergaster* really may have emphasized the digging, transport, cooking, and sharing of deeply buried tubers in their subsistence adaptations. Others have used the Swartkrans evidence to suggest that both early *Homo* and robust australopithecines had bone tools for leatherworking and made little leather bags in which to carry them. Early *Homo* may have been mighty hunters of large animals, brandishing fire and throwing wooden spears or handaxes at their unfortunate prey. They may even have made representational animal art of pecked and flaked stone. All of these stories have appeared in the literature, and the list of behavioral possibilities could obviously be expanded.

Restricting the above list to interpretations of technological and subsistence-related behavior, it could be suggested that much of the familiar human behavior characterizing modern foragers actually existed in the early Pleistocene. This is, in effect, what Glynn Isaac said in the 1970s in his influential but criticized home-base and food-sharing model (Isaac 1978). In that model, Isaac envisioned a gender-based division of labor with the women gathering plant foods and the men hunting for animals, with food surpluses being transported to home bases for sharing later in the day. The present authors have simply specified the plant food, warmed it over with fire, and having accepted at face value highly problematic evidence of digging as tuber digging and of fire as controlled, tuber-cooking fire, served it all up as the cooked-tuber story. A recent revision of the home base model more prudently combines primatological and archaeological evidence as the resource-defense model and explicitly does not accept division of labor as documented in the early Pleistocene (Rose and Marshall 1996).

The cooked-tuber story could be strengthened by addressing the following issues: Why is there abundant evidence of hunting and some form of scavenging, carcass transport, butchery, and sharing and consumption of meat and fat in the behavioral and dietary adaptations of early Pleistocene *Homo* (e.g., Oliver, Sikes, and Stewart 1994 and references therein)? Why are the earliest stone tool kits of the Oldowan dominated by sharp-edged cutting tools? Why is there intensive meat polish on the edges of stone flake knives studied for microwear (Keeley and Toth 1981)? Why is there not microwear evidence of grit or sediment damage on the teeth of supposedly tuber-eating hominids themselves, including the robust australopithecines (Kay and Grine 1988)? I hope that the response will not be that the real function of early stone knives was to peel tubers and thereby remove adhering grit before chewing occurred. If the control of fire and the cooking of tubers existed in the early Pleistocene and contributed in any significant way to the early evolutionary trajectory of the genus *Homo*, why is there no compelling evidence from other sites of the period, including Olduvai, where conditions of preservation were far superior to those at the sites mentioned above? The same question could be posed regarding bone scratching tools and heavy-duty digging tools. Finally, the authors' claims for the nutritional yields from collecting and eating cooked tubers seem to rely on gross tuber weights, not on bioavailability, and will require reevaluation. Gross weights can greatly overestimate the caloric content of high-fiber foods when any portion of fiber is included as bioavailable (Murray et al. 1999). The risk of such inclusion is especially great in the tubers eaten by the Hadza, where fiber content has been reported to be significant (Vincent 1984, 1985).

What is documented in the archaeological record associated with early *H. ergaster* is abundant cut-up, butchered bones of large animals. Let us not lose sight of that evidence. If Wrangham et al. take that to mean that early Pleistocene *Homo* used digging sticks, tuber gathering, and tuber cooking and sharing to support a marginal investment in meat eating and that such an emphasis on cooked tubers selected for the brain expansion, body size increase, tooth reduction, and gut reduction that characterize early *H. ergaster*, then I must suggest that their story is unconvincing.

EUDALD CARBONELL ROURA
Departament d'Història i Geografia, Universitat Rovira i Virgili, 43005 Tarragona, Spain. 6 v 99

Wrangham and colleagues develop a very interesting equation to explain the emergence of complexity in human evolution: cooking of underground storage organs equals tooth reduction, reduced digestive effort, expansion of the brain, new mating structures, and sexual division of labor. *Homo erectus* is considered responsible for this equation. The hypothesis is of course very interesting, and obviously we agree that African *H. erectus* presents a series of features that make it more human anatomically and behaviorally, to the point that Wood and Collard (1999) consider it the earliest hominid species to be assigned to the genus *Homo*. However, we have postulated that technical selection as a form of hominid adaptation had generated behavioral complexity and emerged with the Acheulean tradition in Africa (Carbonell et al. 1999). The reduction of sexual dimorphism and complex behavior reached their first threshold when long and complex logical chains were developed for artifact production 1.6 million years ago. Consequently, from our perspective, cooking has nothing to do with brain expansion and sexual behavioral change. There is no direct or indirect evidence of this activity in the African Lower Pleistocene record.

We believe that the climatic change occurring during the late Pliocene on the African continent, which caused change in the vegetation from tropical forest to wooded savanna, had more to do with the emergence of tools and their utilization by the hominid primates. The consolidation of this adaptation formed the basis for intraspecies social changes (Kimbel 1991). The complexity that undoubtedly appeared with this extrasomatic adaptation is at the base of sexual relationships and mating complexity.

The first stone artifacts were the sign of the appearance of new practices in meat acquisition and consumption in the Eastern African ecosystems (Kibunjia 1994). Nevertheless, it was only 1.6 million years ago, with the appearance of mode 2 or Acheulean technology, that a rupture occurred and hominization was transformed into humanization, with increased inter- and intraspecies competition between hominid primates. Technical selection acquired more and more power within the framework of natural selection, to the point that a division of labor emerged.

The emergence and consolidation of artifact production by the genus *Homo* are irrefutable evidence, dated to the late Pliocene and early Pleistocene, of the systematic consumption of ungulate meat. Cut marks on bone surfaces indicate the consumption of animal tissues by the earliest hominids (Bunn and Kroll 1986). But, as the authors point out, consumption of meat would have been marginal. The striations present on dental remains confirm that hominids were first herbivores and that plant food represented an important proportion of their diet. Although consumption of animal carcasses was marginal, the organization for acquiring them may have been so complex as to influence intraspecies relationships, especially in reference to its distribution (Isaac 1978).

With regard to the consumption of underground storage organs by *H. erectus* we also have nothing to say. Nevertheless, their cooking is a different matter. Evidence of the presumed control of fire at Koobi Fora (Bellomo 1994) and Zhoukoudian (Weiner et al. 1998) is not strong, and these fires have been dismissed as natural in origin. For the moment, the earliest known hearths dated securely are those of Menez-Degran 1, which may be between 350,000 and 500,000 years old (Monnier et al. 1994).

In our opinion, without systematic control of fire it is not possible to develop the complexity proposed by the authors. The systematic control of fire leaves a series of easily detectable empirical records, including thermally induced color change, burned bones, associated blocks, and in some cases ashes. These elements have not been found so far in any Lower Pleistocene site. Even *H. antecessor*, discovered in Atapuerca, did not have fire (Carbonell et al. 1995). Neither in Europe nor in Asia are hearths older than a half-million years.

If this is true, it is difficult to argue that the use of fire for cooking caused changes in sexual and economic relationships and created links explaining the scrounging hypothesis as a dynamic towards the complexity of the human family. We do think that fire energized human society in the Middle Pleistocene, given that it was used in a number of activities such as obtaining warmth, confronting carnivores, artifact production, and lighting and undoubtedly had particular influence on relationships within nuclear human groups.

We agree with some of the ideas expressed in a recent paper published in *Science* (Pennisi 1999), but we are skeptical about the role played by cooking among *H. erectus* in the Lower Pleistocene because of the lack of empirical data. Consequently, we believe that when cooking began some of the most important male-female and female-female relationships already existed. Cooking, clothing, and burial of the dead are more modern acquisitions, and when these occurred there was no important sexual dimorphism.

K. HAWKES, J. F. O'CONNELL , AND
N. G. BLURTON JONES
Department of Anthropology, University of Utah, Salt Lake City, Utah 84112 (Hawkes and O'Connell)/
Department of Anthropology, University of California, Los Angeles, Calif. 90024, U.S.A. (Blurton Jones).
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Wrangham et al. are persuasive about the importance of cooking in human evolution. We agree that new ways of using plant foods probably explain *erectus* body size, digestive anatomy, *and* success in colonizing new habitats (O'Connell, Hawkes, and Blurton Jones 1999); that costs and benefits of resource defense are key factors in the evolution of human sociality (Blurton Jones 1987, Hawkes 1993); that hypotheses other than paternal provisioning will better explain the evolution of both human hunting and pairing (Hawkes 1990, 1993, 1999; Hawkes, Rogers, and Charnov 1995; Blurton Jones et al. 1999); and that archaeological visibility is commonly confused with economic importance in standard arguments about the role of meat in Lower Paleolithic human diets. This is substantial common ground. We are delighted with the company.

Differences between hypotheses we favor and those offered here are also notable. Wrangham et al. argue that an increase in the quantity of nutrients available to those who could fully exploit underground storage organs accounts for increased female body size in *erectus*. But among primates generally, more food means not only greater body mass but also earlier maturity. The larger body size of *erectus* goes with *delayed* maturity (Smith and Tompkins 1995, Hawkes et al. 1988). Something besides more food is needed to explain these changes.

Many underground storage organs not only present metabolism barriers but also defend themselves by growing well below ground. Nonhuman primates *and young human children* have difficulties not only cooking but also digging up deeply buried tubers (Blurton Jones, Hawkes, and O'Connell 1989, 1997). Our hypothesis about the evolution of *erectus* turns on the life-history consequences of using resources that youngsters cannot acquire and process efficiently on their own (Hawkes, O'Connell, and Blurton Jones 1997, Hawkes et al. 1998). In nonhuman primate species, juveniles feed themselves. Genus *Homo* mothers could only take advantage of resources their children could not handle if they acquired and processed the foods for them. Doing so would have allowed the use of new habitats and also set off a cascade of systematic adjustments in life histories. With regular mother-child food sharing, senior females whose fertility was declining could have increased their own fitness in a novel way. By provisioning grandchildren, they would have allowed their daughters to have the next baby sooner. More vigorous older females would thus have raised the fertility of younger kin. Higher fertility in young females—funded not by their own reproductive effort but by that of their mothers—would have enhanced the fitness benefits of vigor at later ages and strengthened selection against senescence. The consequent increases in longevity would in turn have favored delaying maturity and thus growing longer to larger body size (Charnov 1993, Hawkes et al. 1998).

If, as Wrangham et al. hypothesize, australopithecines used deeply buried underground storage organs, then we are wrong about either (1) the handling difficulty we expect those foods would pose for just-weaned youngsters or (2) the life-history consequences of mother-child food sharing. If, however, we are correct that the use of such resources promotes the evolution of *erectus*, changes in social organization different from those favored here by Wrangham et al. are also implied. In most primates feeding competition limits female group size. Wrangham himself has long argued that it is reduced feeding competition among bonobos that allows females to form the alliances that distinguish sexual strategies in that species from those of common chimpanzees (e.g., Wrangham 1986, Wrangham et al. 1996). Reliance by *erectus* on locally abundant underground storage organs would mean not only reduced feeding competition but nutritional *benefits* to females for proximity with female kin. Maturing daughters could increase their fitness by helping to feed younger siblings; aging mothers could help the children of newly maturing daughters. Females who grouped with female kin would do better than those who sought a male bodyguard instead. We agree with Wrangham et al. that mate guarding is more likely than paternal provisioning to explain the evolution of pairing in moderns (Hawkes, Rogers, and Charnov 1995, Hawkes 1999, Blurton Jones et al. 1999). But reliance on underground storage organs would have promoted female grouping patterns in *erectus* that Wrangham et al. pass over as improbable alternatives to the form of the bodyguard hypothesis they propose here.

Paradoxically, as Wrangham et al. note, plant foraging strategies may explain the increased archaeological evidence for carnivory in the early Pleistocene, especially for reasons they do not mention. Larger groups of larger-bodied hominids should have been better at competitive scavenging than australopithecines. Earlier access to carcasses would have meant more meat and more archaeological evidence of meat eating, but that need not mean that meat was a major part of early human diets, let alone the evolutionary catalyst widely assumed (O'Connell, Hawkes, and Blurton Jones 1999). Even modern foragers, skilled and effective at competitive scavenging and eagerly pursuing every opportunity, earn too little from this activity to provide more than the occasional windfall (O'Connell, Hawkes, and Blurton Jones 1988). It is unlikely that early humans, lacking the advantage provided by effective projectile weapons, did nearly as well, let alone any better.

All that said, we reiterate enthusiastic support for more work along the lines developed here by Wrangham et al.

W. C. MCGREW
Anthropology and Zoology, Miami University, Oxford, Ohio 45056, U.S.A. 20 IV 99

Wrangham et al.'s "theft" hypothesis for hominization (although more aptly termed the antitheft or Man-the-Security-Guard hypothesis) is an ingenious weaving together of diverse features: decreased body-size dimorphism, control of fire, dental reduction, enhanced female sexual receptivity, and pair bonding. All of these evolutionary trends are linked to cooking, and the resulting package is said to explain the archaeological and palaeontological record better than do the existing alternatives of Man-the-Provider or Man-the-Bodyguard.

Various questions emerge: First, cooking is never defined in the article, although it is strongly implied that it has to entail the application of heat to foodstuffs. This narrow sense of the term is important, since any causal link to the control of fire depends on it. A broader definition of cooking, such as external transformation of food to a more edible state, might be preferable, since none of the five proposed advantages of cooking is limited to heating. Husks or shells can be cracked by percussion, cell walls can be burst by pulverizing, proteins can be denatured by marinades, toxins can be diluted by soaking, etc. Cooking likely predates fire, just as it now remains independent of it.

Second, throughout the article, faunivory is confounded with carnivory, as if all animals consumed were vertebrates. This narrowing of prey to large packets of flesh elevates hunting (or scavenging, but the latter is barely mentioned) at the expense of collecting (or gathering) other animal matter, especially arthropods and mollusks. This matters because these animal prey can be harvested independently by females with the appropriate technology. Some invertebrate prey, for example, the dispersing reproductive forms of social insects, are of higher energetic quality than meat. The highest-calorie food in nature per unit mass may be honey, not filet mignon or bone marrow. Given the contribution of in-vertebrates to the diets of tropical hominoids and foragers today, it seems unrealistically restrictive to posit an Early *Homo* diet that is devoid of faunivory as the starting point, as in the authors' table 2. There is more to faunivory than meat (see McGrew 1999 for details).

Third, the crucial technology to convert a forager from eat-as-you-go to take-home-some-to-share is, of course, the container. Once the container has been invented, so that small items can be amalgamated for transport, processing, and storage, many of the features assigned to cooking by Wrangham et al. can be equally well explained. Resources can be collected, concentrated, and held and can be stationary or mobile. The resulting large patch enhances the value per food item, given greater energetic efficiency in consumption. Thus, the conditions for males' thieving from females may not have required control of fire or cooking. Or, in a more egalitarian scenario, men may hunt meat to swap for women's collected products, both plant *and* animal. Women may more often provision men than vice versa because of division of labor based more on reciprocity than on coercion (McGrew 1979).

KATHARINE MILTON
Department of Environmental Science, Policy, and Management, Division of Insect Biology, University of California, Berkeley, Calif. 94720-3112, U.S.A. (kmilton@socrates.berkeley.edu). 23 IV 99

This paper appears to be a classic case of too many cooks' spoiling the broth. Though I have high regard for the scholarly work of the authors, the synergism of their union here has produced what amounts to little more than a just-so story. They have homed in on a highly improbable idea—cooking as the key selective element in the initial evolution of *Homo*—and then mustered information to try to support it. I will address a few of the main points to illustrate some of the problems I find in their approach.

A paper using cooking as the key selective element for human (*Homo*) evolution should provide data to support this idea as well as specify when controlled use of fire for cooking appeared. This one provides us with no new data—rather, it recirculates the few data published by others who have already explored evidence for controlled fire and its use by early humans but generally reached different conclusions. In "Fire and Its Role in Hominid Lifeways" Clark and Harris (1985:22) pointed out:

> It would not be difficult to make equally as strong a case for its having been fire—every bit as much as food sharing or meat-eating or a new form of sexual behavior—that helped to weld early hominid groups into the coherent family units that are characteristic of human society. That it has not been thought of as such is surely due to the fact that the evidence of fire has not generally survived . . . What is now needed is systematic study and analysis of [the occurrences of fire], together with experimentation to determine evidence of combustion, temperature ranges, variation in the structure and form of fire-related features, and also whether artifacts and bone can be shown to be significantly related to some of the latter.

Wrangham et al. have not followed these suggestions. The sites they offer to support the use of fire for cooking by human ancestors are by and large the same sites discussed and dismissed as inadequate by Clark and Harris almost 15 years ago. If humans were routinely cooking foods between 2.5 and 1.5 million years ago, the archaeological record should show more evidence of habitual use of controlled fire. It does show many bones split by stone tools, apparently to extract the marrow, but bones show no evidence of having been cooked or roasted (e.g., de Heinzelin et al. 1999). The burned bones at Swartzkrans are not evidence of cooking or roasting (White 1992).

Demmett and I (Milton and Demmett 1988) have suggested that the use of tools by early humans to process and refine foods (both plant and animal) before they were ever brought into contact with the teeth and digestive tract of the feeder led to a reduction in tooth (and gut) size in the human (*Homo*) lineage. Armelagos et al. (1984) discussed evolutionary changes in the craniodental remains of post-Pleistocene Nubian populations during the past 12,000 years. These remains show a reduction in the muscles of mastication and in tooth size and tooth complexity, resulting in changes in the entire craniofacial complex. These modifications were suggested to stem either from a change in diet (reduction of dental attrition) and the increased intake of cariogenic foods, leading to selection for smaller and morphologically less complex teeth, or from diet changes due to the intensification of agriculture that produced less neuromuscular stress on teeth (Armelagos et al. 1984; see also Carlson and Van Gervan 1977). No comment was made about the possible effects of cooked foods on these morphological changes. Furthermore, it is likely that foods were being cooked by human populations in this same region both prior to and after 12,000 B.C. Selection can clearly favor a reduction in tooth size for many reasons other than consuming cooked foods. At some point, the cooking of foods may well have been a contributing factor in human tooth size reduction, but, as these examples make clear, not necessarily.

Surely any species whose females are sufficiently intelligent to collect foods whose nutritional values are enhanced by cooking and then prepare and cook them is hardly likely, simultaneously, to be so primitive that said females must seek protective bonds with aggressive males to protect their cooked delicacies from being stolen! Why are stocks of cooked foods any more likely to be stolen than stocks of raw ones? What are males eating while females discover how to use fire and cook these unspecified foods? Wouldn't battles by males to protect cooked foods select for much the same physical features as battles by males to protect access to estrous females?

Wrangham et al. also fail to point to a single species or genus of wild plant food as a potential cooked item of diet for early *Homo*, though they must know that not all plant parts are the same in terms of nutrients or digestibility. In general, underground storage organs are low in nutrients and serve largely as sources of energy, and humans require a rich repertoire of other nutrients to survive (Milton 1999). Nor, as they themselves note, is it necessary to cook many plant foods, including various underground storage organs, in order to digest them efficiently. For example, raw corn and wheat starches fed to human subjects to test their digestive efficiencies on such substrates were completely assimilated, and no traces of them could be found in feces (Langworthy and Deuel 1920). The digestibility of raw potato starch in these subjects ranged from 62 to 95%, with an average of 78%. Most important, human subjects experienced no discomfort as a result of the ingestion of large amounts of raw starch, nor was the digestibility of other dietary constituents affected (Langworthy and Deuel 1920). For these reasons, it seems imperative for Wrangham et al. to be more precise about the types of underground storage organs or plant foods they have in mind with regard to their cooking scenario.

Although they do mention some cultivated plant species—e.g., manioc, potatoes, soybeans—it is not possible that early human ancestors were utilizing these cultivars in their diet (indeed, potatoes and manioc were domesticated in the New World). Only around 3000 B.C. did the Chinese discover techniques for deactivating the anti-trypsin factor (ATF) in soybeans (which cannot be accomplished by ordinary cooking), with the result that first the beans and then, some 2,000 years later, the bean curd could become dietary staples (Katz 1987). It is highly unlikely that female human ancestors, while defending their unspecified cooked foods from plundering males, were at the same time carrying out a highly elaborate multistep detoxification process on items such as soybeans or bitter manioc.

There is a way to improve the digestion of and hence the nutrient returns from some wild plant foods available to the earliest humans, and this is grinding or reducing them to very fine particles. The high digestibility of the uncooked (raw) wheat, corn, and potato starches discussed above was probably due in part to the fact that these materials were finely ground. Morris, Trudell, and Pencovic (1977) found that cats (obligate carnivores) digested the starch of ground raw maize with considerably higher efficiency when it was finely ground rather than coarse. Raw starch from coarsely ground wheat was less digestible than that from finely ground wheat. Most important, starch from cooked coarsely ground wheat or maize was not digested to a greater extent than starch from these raw grains when finely ground (Morris, Trudell, and Pencovic 1977). These facts too suggest that Wrangham et al. need to devote more thought to the types of underground storage organs or other plant foods required to substantiate their cooking scenario.

The latter portion of the paper deals loosely with sexual dimorphism, and features of human and chimpanzee sexual receptivity. While their argument is not entirely clear to me, Wrangham et al. seem to suggest that modern humans are large and should therefore show more sexual dimorphism in body size than they do. Modern humans and common chimpanzees have effectively the same body-size dimorphism, but, contrary to statements in this paper, many modern human populations do not differ significantly in absolute body mass relative to common chimpanzees (Clutton-Brock and Harvey 1977, Milton 1983). Furthermore, if common chimpanzees and bonobos, which have the same pattern of body-size dimorphism, do not accurately reflect the relationship between female sexual receptivity and sexual dimorphism Wrangham et al. propose, how can they extend the pattern of sexual receptivity seen in modern humans back in time to *Homo erectus*?

I have pointed out a sufficient number of problems with this paper that readers should proceed with care. "Demonic males" (cf. Wrangham and Peterson 1996) seem to have spawned demonic meals—leading to a good case of indigestion!

RALPH M. ROWLETT
Department of Anthropology, University of Missouri, Columbia, Mo. 65211, U.S.A. 21 V 99

Wrangham et al. evince a certain indecision about those aspects of their theory that depend upon the availability of controlled fires to *Homo erectus*, even though cooking is critical for that theory. Although anthropologists have been reluctant to allow the control of fire by such early humans, a number of sites indicate that *H. erectus* had the ability to produce and control fire. In addition to the African sites of Chesowanja, Gadeb, and Swartkrans, Koobi Fora on Lake Turkana presents extremely good evidence for the use of fire by *H. erectus*, even in the early phase sometimes called *H. ergaster*. These ostensible fireplaces have been extensively scrutinized independently by Randy Bellomo and Michael Kean (1991, 1994) and by me working with several different colleagues, generously aided by the Wenner-Gren Foundation. Bellomo's archaeomagnetic work at locality FxJj 20 Main is cited with some explication, while the other studies are more summarily mentioned (Harris 1978). Since Harris first wrote, these studies have removed all doubt that even early *H. erectus* had the technological capability of cooking foodstuffs.

The Koobi Fora fireplaces are inverted-lens-shaped reddish patches in the Okote Tuff, dated by K/Ar to ca. 1.6 million years (Isaac and Harris 1997:160–62). Charles Peters and I have used thermoluminescence (TL) to demonstrate that the reddish patches at FxJj 20 East were heated more recently than the surrounding tuffs and not the result of either fungal invasion or precipitation of iron particles (Rowlett and Peters n.d., Rowlett 1986). Comparison with lightning strikes in Africa, Georgia, and Kansas City showed that the 40–50-cm fireplaces were not due to lightning, which seldom leaves a fulgurite with a diameter exceeding a centimeter. In an actualistic study we burned modern silver maple stumps in Missouri and then excavated the remains to find that the resulting stellate burned areas contrasted with the basin-shaped reddish patches. Finally, differential thermal analysis showed that the fires that caused the reddish patches were not as hot as lightning-caused or iron-smelting fires, attaining temperatures just under 400 °C.

Robert Graber, Michael Davis, and I later addressed the question of distinguishing fireplaces from burned trees (Rowlett, Graber, and Davis n.d.), making simple actualistic hearths and burning trees in a modern savanna-like open woodland. Our thought was that the phytoliths of burned trees should be much more homogeneous than the phytoliths in fireplaces, which would probably have involved different kinds of sticks and woods and in some instances grass and other tinder. The phytoliths found in the Koobi Fora patches do indeed show this heterogeneity, even more than our experimental fireplaces, built by college students unaware of the implications of the kinds of fireplaces and stump burnings that they were instructed to make. The results of these studies have already been published (Rowlett 1990). Of the four patches found at FxJj 20 East (Isaac and Harris 1997:fig. 4.29, pl. 4.14), three fit the fireplace model, while an irregular, narrow one does indeed seem to be a burned tree.

An illuminating outcome of these phytolith studies is that much of the fuel was palm wood. Epie Pius, a Bukasi anthropologist, asserts that palm-wood fuel is chosen where ease of ignition and height of flame may be important. Because it burns rapidly, a fire of palm wood requires intermittent tending. The choice of easily lighted palm wood, with its troublesome need to be tended, implies that fire ignition was a concern of *H. erectus/ergaster* at Koobi Fora. The tall flames would have helped make the fires effective for predation prevention, as Clark and Harris (1985) and Bellomo (1994) have emphasized. The latter's archaeomagnetic techniques revealed that the fires on the reddish patches burned more than once and must have been rekindled somehow.

Our current experiments center on the work required to keep a largely palm-wood fire going and on how easily various woods can be set ablaze. We are also studying additional basin-shaped reddish lenses excavated at other localities in the Okote Tuff by Harry Merrick to determine which of these may be fireplaces.

Stone artifacts are found in and around the fireplaces at Koobi Fora FxJj 20 East. While most are basaltic, Isaac and Harris (1997:163–64) emphasize that an unusual number of them are made of chert, a prime material for striking sparks to start fires. Blackened and reddened cherts seem to have been heat-altered. Some of the basaltic flakes have also been affected by heat; their TL response is lower than the expected geological one (Rowlett 1990). A roughly denticulated cutting flake with a TL response indicative of its having been heated was found in the fireplace beside the robust australopithecine mandible KNM-ER 3230 (Wood 1991:161–64; Isaac and Harris 1997:160). The close association of the cutting tool and the fossil mandible suggests the cooking of meat.

These researches make it clear that *H. erectus/ergaster* at Koobi Fora not only controlled fires but probably could create them and had food closely associated with the fireplaces. They clearly had the technological capability of cooking tubers and other foodstuffs. The question is whether they did so. If tubers were cooked, some of them would undoubtedly have been burned. Although charcoal has not survived, these ancient fireplaces contain many tree, grass, monocot, and other unidentified plant phytoliths, some of which might represent the stems, epidermis, and other parts of tuberous plants containing phytoliths or identifiable microparticles. Given the critical significance of the cooking of foraged foodstuffs for Wrangham et al.'s explanation of human bonding and mating systems, we intend to expand our research program on the fireplaces and the surrounding tuff matrix to test the hypothesis that early *H. erectus/ergaster* was already cooking tuberous plants.

B. HOLLY SMITH
Museum of Anthropology, University of Michigan, Ann Arbor, Mich. 48104, U.S.A. (*bhsmith@umich.edu*).
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With *Homo erectus* comes a hominid much different from *Australopithecus* and even *H. habilis*. As Wrangham et al. point out, a host of features point to a major adaptive shift: larger brains, larger body size, proportionately and absolutely longer legs, smaller cheek teeth, a more human-like thoracic shape, and the appearance of the Acheulean tool industry. I would add that the dental maturation of *H. erectus* is shifted toward a human pattern, a gross sign of shifting maturation rate not evident in *H. habilis* (Smith 1993). Even conservative interpretations of the evidence point to a major shift in subsistence and social dynamics of early *H. erectus*: larger brains, smaller teeth, and a thoracic shape corresponding with gut simplification all point to a higher-quality diet (Aiello and Wheeler 1995); reduced sexual dimorphism points to altered social dynamics (Mitani, Gros-Louis, and Richards 1996); brain and body size increase and slowing maturation hint at increased juvenile survival (Promislow and Harvey 1990).

What kind of shift could have had such an impact? Here, Wrangham et al. propose that cooking, particularly of tuberous plant foods, fills the bill.

Before weighing present evidence, I can add more from close comparative study of teeth. Two key fossils offer a rare chance to compare dental attrition in individuals closely matched in dental development: the type specimen of *H. habilis*, OH 7, and the Nariokotome *H. erectus* youth, KNM-WT 15000. Mandibles are well described and illustrated in Tobias (1991:486–514, pls. 66–83), Brown and Walker (1993:figs 8.2–8.3), and Smith (1993: fig. 9.1). Each mandible has I_1–M_2 erupted; M_2 root development is about half complete in Nariokotome and half-to-three-quarters complete in OH 7. The two juveniles correspond approximately to human 11-year-olds but in all probability matured more quickly than humans and were likely closer to 8–9 years of age at death (Smith 1993).

Despite permanent teeth worn for five years or less, OH 7 exhibits a great deal of wear. Dentin is well exposed on all four incisors. The thickly enameled cusps of M_1 are pounded almost flat, exposing dentin on the two buccal cusps. Despite the fact that the OH 7 cheek teeth (P_3–M_2) are 129% the area of those of Nariokotome, the latter shows far less wear. Central incisors of Nariokotome have two tiny dentin exposures, and M_1 cusps are only lightly blunted with wear. If, as seems likely, *H. habilis* matured slightly more quickly than *H. erectus* (Smith, Gannon, and Smith 1995), then one can say that OH 7 has *more wear on larger teeth in less time* than Nariokotome.

Comparison with australopithecine juveniles is hampered because most are infants or young children, but, roughly speaking, the high wear of OH 7 is more on a par with that of the MLD 2 *A. africanus* (see Tobias 1991: pl. 68) than with that of Nariokotome (although the comparison is imperfect because MLD 2 is younger). A preliminary comparison with prehistoric humans using data in hand (see Smith 1983) puts OH 7 near the top of the hunter-gatherer range and Nariokotome at low/average in degree of wear for age, a comparison that should hold whether or not one adjusts for species differences in rate of maturation.

Lastly, although the cheek teeth of *H. erectus* are much reduced from *H. habilis*, the anterior teeth are not (Calcagno and Gibson 1991). Indeed, *H. erectus* maintains the widened incisor battery of *H. habilis* (see also Tobias 1991:784), a battery well suited to biting, slicing, and tearing. In sum, teeth suggest that *H. erectus* still needed slicing incision but that compared with that of *H. habilis* its food needed much less chewing and produced much less wear on incisors and molars.

What sort of food fulfills the requirements? Uncooked meat is a good candidate. While cooking would also reduce forces on the dentition, simple cooking in hearth ashes, such as that of Australian Aborigines, introduces much grit into food and produces high attrition (Campbell 1939). Similarly, the later Paleolithic, where cooking is undoubtedly present (Brace 1996), seems to have high levels of dental attrition (e.g., Trinkaus 1983). Thus, tooth wear and proportion, added to the long-legged striding skeleton, lead me to favor a hunting strategy for *H. erectus* with increased meat in the diet.

Tooth wear of early *Homo* needs more attention than this short descriptive essay, but given preliminary evidence I wonder if Wrangham et al. can imagine cooking at a *simple* technological level that lessens, rather than adds, abrasives? In any case, the true value of an article like this is to attempt to explain how fundamental innovation in social structure can follow from basic change in subsistence and to marshal and focus our evidence to create testable hypotheses. This article shows that we are at a level of evidence and theory that promises a real advance in our understanding of the hominid fossil record.

Reply

RICHARD W. WRANGHAM, JAMES HOLLAND JONES, GREG LADEN, DAVID PILBEAM, AND NANCYLOU CONKLIN-BRITTAIN
Cambridge, Mass., U.S.A. 15 VI 99

Our thanks go to the commentators for clear thoughts and horrendous puns. They have produced enough material that, if we chose to digest each empirical challenge, our response would be far too long. In our model, we suggest that cooking underground storage organs could substantially increase the total available energy of a hominid diet without increasing relative foraging costs. The increase in body size and reduction of dimorphism with the rise of the genus *Homo*, implying decreased intrasexual mate competition among males, may be a signal of the beginning of cooking. The behavioral changes required for cooking lay the foundation for a producer-scrounger dynamic. At the outset, females would have paid relatively greater fitness costs in losing their produce to theft by larger, dominant males, so selection favored females who obscured their reproductive cycle, favoring pair-bonding and thus alleviating the costs of scrounging. This reduction in cost occurred because pair bonds meant two individuals to defend a hearth and removed males from the pool of potential scroungers. On the basis of our current understanding of the fossil record, no other period in the evolution of the genus *Homo* produces the magnitude of evolutionary signal that we expect from the adoption of cooking.

The point of our article was not to claim proof. Instead, we argued the value of our scenario because it incorporates variables that have previously been ignored, fits the data at least as well as previous stories, and makes testable predictions. Therefore we agree with the thrust of much of the commentary—that the fossil and archaeological records are too severely edited to allow refined tests of either the cooking or the meat-eating hypothesis. With Hawkes et al., Rowlett, and Smith, we look forward eagerly to further evidence on the many unsettled topics, such as the uses of controlled fire, the nutritional gain from cooking, the sources of body-mass increase, and the causes of tooth-area decrease.

Some respondents (Brace and Milton) question the value of our scenario, defaming it as a just-so story, but one person's just-so story is another's hypothesis. We prefer to think of our proposal as a model that organizes diverse threads of information to generate testable hypotheses. Whether our proposal turns out to be right or wrong, we hope that discussions of hominization will increasingly incorporate the selection pressures on females, the significance of sexual dimorphism in body mass, the role of plant foods in the diet, and the potential for competitive relationships between the sexes. This is more than just political correctness. For several decades behavioral ecologists have argued that ecological pressures on social systems are mediated particularly acutely through their effects on females. (This is so wherever there exist asymmetries in reproductive investment between the sexes; in such cases the more heavily investing sex becomes a limiting factor in the reproductive success of the less-investing sex [Trivers 1972].) Paleoanthropology must do more to incorporate the concepts of modern behavioral and evolutionary ecology.

Brace describes a variety of changes in the inferred life history of *H. erectus* including larger female body size, larger brain size (which is correlated with age at first reproduction), longer gestation, and increased life expectancy. He suggests that giving birth to a larger-brained neonate following a long gestation is sufficient to explain the larger size of *H. erectus* females. We would ask, what selective regime favored longer gestations and larger size?

We suggest that cooking, by both increasing expected energy gain and reducing variance in energy gain, would have lowered adult mortality rates, favoring longer life span and increased body size. Furthermore, the changes in energy gain could have favored faster juvenile growth rates, later ages at first reproduction, or both, precipitating larger size at maturity (Abrams and Rowe 1996, Abrams et al. 1996; see also Janson and van Schaik 1993).

An increase in female attractiveness does not depend directly on average female body mass as Brace suggests. By extending their period of potential sexual receptivity, *H. erectus* females tipped the scales in favor of pair bonding, lowering the OSR. As a response to lowered adult mortality rates and increased energy gain during the juvenile period, female body size increased, and there was no concomitant increase in male size because of the low OSR, which would have reduced the benefits to males of relatively large size.

Carbonell lists innovations that occurred in the hominid line between the last common ancestor of chimpanzees and humans (e.g., cooking, clothing, burial of the dead, creation of flaked stone tools, and changes in female-male social and economic dynamics) and suggests that these changes occurred during the Middle Paleolithic. If this proposition is true, why was there such a dramatic reduction in sexual dimorphism much earlier? The strength of our model is that it provides an explanation that links cooking and change in socio-sexual dynamics in a way that is consistent with both the fossil record and behavioral ecological theory. Carbonell fails to link the selective forces shaping tool use with a change in sexual dimorphism or socio-sexual dynamics.

Several commentaries imply that cooking and meat eating should be seen as mutually exclusive alternatives in terms of their importance for hominid evolution (Bunn, Brace, Milton). We disagree. The evidence of cutmarks on bone around 2.5 million years ago suggests that late australopithecines were obtaining important nutrition from large mammals, probably a new source for them. Food from large mammals may have contributed to the brain-size increase in *Homo habilis*. But the major signals of improved nutrition did not evolve until about half a million years later, when they are seen in the larger female bodies and smaller teeth. Unless new fossil evidence changes this picture, it means that large-mammal eating preceded the evidence of hominization by too long to be directly responsible for it. Two processes therefore appear to have occurred—the development of large-mammal eating (with its relatively muted effects, at least initially) and something else (responsible for the major events of hominization).

Our proposal for the "something else," the use of fire to prepare plant foods, it not the only possibility. McGrew implies that other kinds of food preparation may have been important. Cooking of meat is another candidate, though our nutritional data suggest otherwise. We welcome the development of alternative scenarios as ways to enrich our thinking about the interaction of nutritional, ecological, demographic, and social pressures.

Bunn and Milton are concerned that we place too much stock in large, deeply buried tubers. Our choice of underground storage organs was, however, deliberate. Large tubers are only one of several kinds of storage organ that hominids could have exploited. Others include the walnut-sized corms of sedges growing in lacustrine mud (Catherine Smith, personal communication) and bulbs, rhizomes, or small tubers in shallow soils.

We share Milton's frustration regarding the lack of chemical and digestibility information on wild roots and tubers. We were forced to use what little we could find in the modern literature comparing cooked versus uncooked foodstuffs. Using modern analytic methods, recent literature contradicts the results from the 1920 paper of Langworthy and Deuel. Evaluating nongrain starch sources, researchers have found that cooking does improve the assimilation of glucose from starch (Vaaler, Hanssen, and Aagenaes 1984, Collings, Williams, and Macdonald 1981).

Regarding the supposed low nutritional value of underground storage organs, chemistry has been published indicating that combinations of them should provide adequate macronutrients. Considering 28 underground storage organs from a woodland habitat in Zambia (Malaisse and Parent 1985), crude protein averaged 8.3% of dry matter (DM) with ranges from 1.0% to 39.2%, indicating that selectivity could easily result in a diet adequate in protein. Domestic underground storage organs (n=19) averaged 7.0% crude protein, ranging from 1.4% to 14.4% (Leung 1968, Watt and Merrill 1963). Adult humans, consuming a low-fat (5% of DM) diet, need only about 9.5% crude protein in their diet (RDA 1980). Wild fat content averaged 4.0% and ranged from 0.3% to 19.8%, compared with the domestics mean of 1.7%, ranging from 0.3% to 20.0%. In addition, the Zambian roots and tubers were all within a potential home range of early humans, facilitating a diet containing various underground storage organs per week and a balanced diet.

Clearly, cooking and the behavioral changes associated with its emergence could allow alloparental provisioning, for example, by grandmothers, as suggested by Hawkes and colleagues. This may be the difference between a human life history, in which postreproductive females can make large contributions to their inclusive fitness through their continued high levels of productivity, and a pilot-whale life history, in which postreproductive females have little to offer in terms of further investment.

We recognize that a weakness of our model is the mixed evidence for controlled fire with *H. erectus*. Rowlett's commentary suggests that this may not be as much of a weakness as we had thought. We think it entirely possible that evidence for fire use in *H. erectus* has been lacking because paleoanthropologists have sought the wrong types of fires. The ephemeral fires used to cook underground storage organs (as, for instance, used by the Hadza) may not produce the hearths characteristic of the temperate Upper Paleolithic (J. F. O'Connell, personal communication; O'Connell, Hawkes, and Blurton Jones 1999). We also recognize that, as suggested by Smith, the tooth-wear evidence is equivocal, and we see further study of this issue as essential.

In conclusion, we have highlighted important problems associated with the origin of the genus *Homo* that have heretofore been ignored by students of human evolution. Some nonhuman animals have encephalization coefficients on a par with modern humans (dolphins, capuchin monkeys) and have been observed engaging in cooperative hunting with subsequent food sharing (chimpanzees), fashioning and using simple tools (chimpanzees), moving bipedally (bonobos, birds, kangaroos), and engaging in strategic alliances between nonrelatives (dolphins). But no other animal has yet been observed to have the social system that characterizes humans, a system that has so far eluded explanation. We look forward to future attempts to interface our model with other explanations that can account for the human social system and the observed changes in life history implied by the fossil record.

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