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## Grandmothering and the evolution of *Homo erectus*

Despite recent, compelling challenge, the evolution of *Homo erectus* is still commonly attributed to big game hunting and/or scavenging and family provisioning by men. Here we use a version of the "grandmother" hypothesis to develop an alternative scenario, that climate-driven adjustments in *female* foraging and food sharing practices, possibly involving tubers, favored significant changes in ancestral life history, morphology, and ecology leading to the appearance, spread and persistence of *H. erectus*. Available paleoclimatic, environmental, fossil and archaeological data are consistent with this proposition; avenues for further critical research are readily identified. This argument has important implications for widely-held ideas about the recent evolution of long human lifespans, the prevalence of male philopatry among ancestral hominids, and the catalytic role of big game hunting and scavenging in early human evolution.

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*Homo erectus* presents an important and challenging problem to students of human evolution. A distinctive, well-defined fossil form, it was far more widely distributed than any previous hominid, extant for more than a million years, and behaviorally different from both apes and modern humans, though in ways that are not yet entirely clear. Conventional wisdom has long associated its evolution and dispersal with big game hunting and paternal provisioning. These practices are thought to have stimulated the development of other modern human-like patterns of behavior, including extended periods of juvenile dependence, central place foraging, a sexual division of

labor, and the nuclear family. Until recently, strong support for this argument came primarily from the archaeological record, particularly from the common association between stone artefacts made by *H. erectus* and the remains of large animals allegedly butchered and transported from kill sites to distant base camps for further processing, sharing, and consumption. The apparent match between this archaeological "signature" and those produced by modern hunter-gatherers led to the inference that other behaviors associated with the latter were also present in *H. erectus*. Key elements of the modern pattern, minus language and certain cognitive capabilities, were projected

well back into the Pleistocene; arguments about the subsequent emergence of *Homo sapiens* were structured accordingly.

Appealing as this argument once was, the results of recent primatological, ethnographic, and archaeological research undercut it. Hunting is now known to be far more common among non-human hominoids than previously appreciated; yet it does not involve paternal investment. Big game hunting among modern tropical foragers, though sometimes productive, has been shown to be a poor strategy for feeding a family. Even the significance of archaeological assemblages formerly seen as providing clear evidence for ancient hunting is contested, some analysts arguing that they indicate little more than passive scavenging at kills made by other predators. If big game hunting, central place foraging, and paternal provisioning are eliminated from the *H. erectus* mix, then support for contingent inferences about modern human-like social organization and mating arrangements disappears. Reconstructions of its behavior are reduced to intriguing but somewhat disconnected inferences based on skeletal anatomy and archaeology; questions about its evolutionary origins and persistence are largely begged.

Here we offer a different model, one that has been foreshadowed in several ways over the past two decades, but only now developed in comprehensive form. We consider the proposition that *H. erectus* evolved as a result of climate-driven changes in female foraging and food sharing practices, possibly involving the exploitation of tubers. These changes may not only have had important effects on ancestral human ecology and physiology, but could also have provoked the first fundamental move away from hominoid life history patterns.

In the following pages, we briefly review the conventional wisdom on *H. erectus* ecology and the current critique thereof. We then turn to our alternative model, organizing empirical and theoretical elements

developed elsewhere in terms of a series of predictions about relationships between past environmental change, adjustments in female foraging and food sharing, and their implications for hominid life history and ecology. We draw attention to recently proposed inferences about *H. erectus* life history; then review the evidence for anticipated climatic, environmental, and economic correlates. Though critical data are patchy, results are generally consistent with expectations. Potentially productive avenues for further research are clearly indicated. We comment on the implications of these results for widely held ideas about a much later date for the first appearance of long post-reproductive human lifespans, and for the notion that male philopatry and female dispersal are basic features of social organization among all members of the African ape clade, including ancestral hominids. We conclude with some remarks on the archaeological evidence that continues to shape conventional wisdom on *H. erectus*.

### ***Homo erectus*: a critique of conventional wisdom**

*Homo erectus* is a large-bodied hominid, similar in size and overall form to modern humans, but with a different cranium and a smaller brain (Rightmire, 1990, 1998; Walker & Leakey, 1993). The earliest examples (sometimes called *H. ergaster*, Wood, 1992) are from Africa, where they date to about 1.8 Ma (Feibel *et al.*, 1989; White, 1995). Near-contemporary specimens may be represented from the Caucasus, south China, and Indonesia (Brauer & Schultz, 1996; Gabunia & Vekua, 1995; Huang *et al.*, 1995; Swisher *et al.*, 1994), suggesting an early spread throughout the Old World tropics and into the temperate zone, a proposition consistent with emerging archaeological data (e.g., Dennell & Roebroeks, 1996; Dennell *et al.*, 1988; Gibert *et al.*, 1998; Tchernov, 1989). Once

dispersed, *H. erectus* persisted, with little change in either physical form or geographical range, into the late Middle Pleistocene (<500 ka), when various populations evolved to or were displaced by *H. sapiens*.

Important inferences about *H. erectus* ecology and life history are drawn from its morphology, especially in contrast with that of contemporary and earlier hominids. Its modern human-like limb proportions are read to indicate fully terrestrial bipedality; its larger body size and more linear form a broader foraging range and higher tolerance for aridity; its thoracic cavity a simpler gut and correspondingly higher quality diet; its reduced sexual dimorphism the presence of multi-male, multi-female social groups; its dental eruption sequence and brain size and age at maturity and average adult lifespan intermediate between those of australopithecines and modern humans (Aiello & Wheeler, 1995; McHenry, 1994; Ruff, 1994; Smith, 1993; Walker & Leakey, 1993).

Until recently, equally important inferences about its behavior were drawn from the contemporary archaeological record. Generally speaking, early Pleistocene archaeological sites are larger in size, more diverse in terms of assemblage composition, and found in a broader range of habitats, both locally and globally, than those of the late Pliocene. Their associated faunal assemblages are often especially striking. Many include the remains of one or more (sometimes many more) large animals, mainly ungulates, often of several species. Many of the bones have been damaged, some by stone tools, apparently in connection with processing for consumption of associated meat and marrow.

These data were formerly interpreted by reference to presumed differences in the behavior of great apes and modern human foragers (e.g., Isaac, 1978; Leakey, 1971; Washburn & Lancaster, 1968; see also Binford, 1981; Fedigan, 1986; Hill, 1982; Isaac, 1984; Sept, 1992 for critical review).

Special attention was drawn to nuclear families, central place foraging, and a sexual division of labor in which men hunt (mainly big game) to provision their wives and children; all thought to be typical of modern hunter-gatherers and pre-agricultural humans in general, but unrepresented among the great apes. Since some of the earliest faunal assemblages contained elements that had arguably been transported from distant kill sites, presumably by males who gave the meat to dependent mates and offspring, then other aspects of modern human behavior might be, and often were, inferred accordingly (see especially Isaac, 1978).

The evolution of this pattern was explained by appeal to a long-term trend toward cooler, drier climate that reduced the availability of previously important plant foods while favoring the spread of game-rich savannas. Ancestral hominid males were thought to have responded by adding large animals to their diets, thereby producing a potentially sharable resource. Hominid females paired with hunters to ensure access to the new food, which in turn enabled them to reduce their own foraging efforts. Nuclear families, a sexual division of labor, and paternal provisioning were established as a result. Female fertility and offspring survivorship were enhanced; an extended period of juvenile dependence, larger brain size, increased learning, and greater behavioral flexibility were all underwritten. Greater ability to cope with environmental variation, significant increases in geographical range, and long-term evolutionary success followed.

Over the past 20 years, this "hunting hypothesis" has been undercut in three important ways:

- Primates, particularly chimpanzees, are now known to hunt often (Boesch & Boesch, 1989; Stanford, 1996; Uehara *et al.*, 1992; Wrangham & Bergman-Riss, 1990). Most hunting is done by males;

the meat obtained is widely shared; yet there is no evidence for central place foraging or paternal provisioning.

- Evidence for pervasive paternal provisioning among modern human hunters has also been challenged (Hawkes, 1990, 1993; Hawkes *et al.*, 1991, 1998). In the best known tropical foraging populations, men consistently pursue large game rather than other resources, despite the fact that returns are *highly* variable in the short run and impossible to defend from other claimants once in hand. If paternal provisioning were truly an important goal, they would do better by spending more time on small game and plant foods, both of which produce more reliable income and are often easily secured for family consumption. The fact that they target either less regularly than would meet this goal strongly suggests that big game hunting serves some other end, unrelated to provisioning wives and children.
- Archaeological evidence for big game hunting and paternal provisioning by *H. erectus* has also been re-evaluated. At some important sites, analysis of damage patterns on bones shows *no* evidence of hominid involvement (e.g., Binford, 1981; Klein, 1987). At others, the data can be read to indicate little more than “passive” hominid scavenging, mainly of long bone marrow and brain cavity contents (Binford, 1981; Blumenschine, 1991; Marean *et al.*, 1992).<sup>1</sup> If accurate, this means that the amounts of edible tissue so acquired were probably too small and obtained too irregularly to pro-

vision juveniles (O'Connell *et al.*, 1988b). Hunting and aggressive scavenging may also have been practised (Bunn & Ezzo, 1993; Capaldo, 1997; Dominguez-Rodrigo, 1997); but even if they were, it is unlikely that they were reliable enough to meet the *daily* nutritional needs of younger offspring, especially since active hunters with better weaponry (bows and poisoned arrows) living in similar habitats today cannot do so consistently (Hawkes *et al.*, 1991, 1998). Finally, there is no good evidence for the transport of meat by early hominids to distant “central places”. The archaeological criteria formerly used to support this inference are now seen to be themselves unsupported (O'Connell *et al.*, 1988a, 1990). Large animals represented in early archaeological assemblages may well have been processed and consumed by hominids at or near the point of initial acquisition (e.g., Marean *et al.*, 1992; O'Connell, 1997).

These observations have very important implications: they eliminate all standard justifications for inferences about nuclear families and a modern human-like sexual division of labor in *H. erectus*. This raises key questions about *H. erectus* ecology and evolution. Current approaches to answering them fall into two categories: (1) those that entail continued insistence on the importance of big game hunting, central place foraging, and the prevalence of near-modern human patterns of social organization and reproduction in *H. erectus*, *despite* compelling challenge (e.g., Gowlett, 1993; Leakey & Lewin, 1992; Stanley, 1996); (2) those that respond to the challenge by treating the archaeological record much more inductively, using recent advances in taphonomy to reconstruct whatever possible about past hominid behavior, but with few exceptions about the shape it might take, apart from being “not modern” (e.g., Bunn & Ezzo, 1993; Potts, 1988; Rogers *et al.*, 1994).

<sup>1</sup>Though it has long been assumed that FLK “Zinj” and other sites of similar age (~1.75 Ma) were produced in part by “early *Homo*” (cf. *habilis*, or more narrowly, *rudolfensis* [e.g., Bunn & Ezzo, 1993]), the earliest dates for African *H. erectus* (*ergaster*) (Feibel *et al.*, 1989; White, 1995) and the coincident change in the archaeological record, marked by a sharp increase in assemblage diversity (compare Bunn, 1994; Kibunjia, 1994), now make it a better candidate for that role.

However commonly adopted, the first approach is indefensible. The second attends to archaeological evidence simply because it is easily recognized and relatively easily interpreted. The goal of accounting for it—of identifying and describing all the processes, human and non-human, involved in its creation—takes center stage. Though there are good historical reasons for the change in focus (compare Binford, 1981; Isaac, 1983), its net effect has been to beg the larger, ultimately more important ecological and evolutionary questions Pleistocene archaeology was once seen to address. The long-running dispute about whether early Pleistocene zooarchaeological assemblages represent hunting or some form of scavenging illustrates the problem. As currently phrased, and unlike the argument originally developed by Isaac (1978), *no other interesting questions about hominid behavior are resolved by the answer*, mainly because they are no longer asked. The only way of identifying such questions, and, by extension, the data pertinent to addressing them, is by developing and evaluating comprehensive models of early Pleistocene hominid ecology and evolution comparable to, but better-warranted than, the now-discredited hunting hypothesis.<sup>2</sup>

### The grandmother hypothesis<sup>3</sup>

One such model, the “grandmother hypothesis”, has so far been developed as follows:

<sup>2</sup>Blumenschine and associates (e.g., Blumenschine & Peters, 1998; Blumenschine *et al.*, 1994) and Rose & Marshall (1996) both take steps in this direction; but in each case the potential impact is limited by the narrow goal of accounting for certain features of the archaeological record (mainly faunal assemblage composition), rather than the larger evolutionary phenomenon of which it is a part.

<sup>3</sup>Two very different versions of the grandmother hypothesis are discussed in the recent literature, one focusing on factors that might favor an “early” end to fertility, the other on the evolution of long post-reproductive lifespans. Here we are concerned only with the latter (see Hawkes *et al.*, 1997; Hawkes *et al.*, 1998b; Kaplan, 1997; Peccci, 1995 for discussion).

- Observations among modern hunter-gatherers show the importance of older women’s foraging when mothers of child-bearing age rely on resources that weaned children cannot handle on their own. This suggests that mother-child food sharing could have favored the evolution of increased post-menopausal longevity that distinguishes humans from other hominoids.
- Several key life history attributes vary systematically with adult lifespans across the mammals generally and among primates in particular. If the underlying tradeoffs hold for humans, and longer adult lifespans are due to grandmothering, then the other departures from “typical ape” life histories that characterize our species may be (unexpectedly) explained as well.
- Since the ecological circumstances that would have favored increased mother-child food sharing and related changes in life history can be specified, the grandmother hypothesis provides the basis for an evolutionary scenario that can be evaluated in light of pertinent paleoclimatic, environmental, fossil and archaeological evidence.

#### *Hadza women’s foraging and food sharing*

Our model is grounded on the results of fieldwork with the Hadza, a small population of traditional foragers living in the arid savanna woodlands of the Eastern Rift, northern Tanzania (Blurton Jones *et al.*, 1996).

Apart from the very old and very young, Hadza of all ages are active, productive foragers. Time allocation and foraging returns are particularly striking for senior females and younger children. Women in their 60s and early 70s work long hours in all seasons, often with return rates equal to (sometimes greater than) those of their reproductive-age female kin (Hawkes *et al.*, 1989, 1995, 1997). Hadza children are

involved in the food quest virtually from the time they can walk, and by the age of five can and do supply, in some seasons, up to 50% of their daily nutritional requirements by their own efforts (Blurton Jones *et al.*, 1989, 1994a, 1997; Hawkes *et al.*, 1995, 1997).

Hadza mothers and grandmothers routinely capitalize on children's foraging capabilities by targeting resources that youngsters can take at high rates, notably fruit. Sometimes this involves bypassing items from which women earn better returns, but that children cannot handle. These choices mark an effort to maximize "team" returns, those earned by women and children together. In the wet season, when fruit is widely available, children's foraging opportunities largely determine adult female foraging strategies (Hawkes *et al.*, 1995).

When resources easily taken by children are unavailable (especially in the dry season), Hadza women provision their offspring with foods they can procure reliably and efficiently. A good example is the woody rootstock, *Vigna frutescens* (Hadza: //ekwa), which favors deep stony soils and requires both substantial upper body strength and endurance to collect and the ability to make and control fire to process. Adult women, including seniors, take it often in all seasons, routinely earning up to 2000 kcal/h as a result (Hawkes *et al.*, 1989, 1995, 1997; Vincent, 1985a,b). Pre-adolescents seldom pursue it, and rarely gain more than about 200 kcal/h when they do (Blurton Jones *et al.*, 1989). Youngsters under 8 years old ignore it entirely.

This provisioning has an important ecological implication: it allows the Hadza to operate in habitats from which they would otherwise be excluded if, as among other primates, weanlings were responsible for their own subsistence.

It also creates the opportunity for another adult to influence a mother's birth-spacing: if someone else supplies food for her weaned

but still dependent child, she can have the next baby sooner. Under these circumstances, grandmother, whose fertility has declined, can have a large impact on her own fitness by feeding the weaned children of her younger kin. Analyses of time allocation, foraging returns, and children's nutritional status (measured by seasonal changes in weight) provide a compelling measure of her effect (Hawkes *et al.*, 1997). In families where mother is *not* nursing, children's nutritional status varies in accordance with mother's own foraging effort. At the arrival of a newborn, however, mother's foraging time drops and the correlation between her foraging effort and her weaned children's weight changes disappears. Instead, those weight changes vary closely with the effort of a related senior female, usually grandmother.

This suggests an hypothesis to account for the differences in average adult lifespans among the hominoids. Child-bearing careers in humans and apes are similar in length, but humans survive far longer after menopause. The dependence of weaned children on food from adults would have allowed ancestral human grandmothers to affect their fitness in ways that other apes could not, increasing the strength of selection against senescence, lowering adult mortality rates, and so lengthening average adult lifespans.

#### *Female food sharing and the evolution of human life histories*

Life histories differ widely among the mammals: some grow fast and die young; others mature slowly and live long adult lives (e.g., Harvey & Read, 1988). Although this variation correlates with body size, relationships among life history features persist even when the effect of body size is removed. Some are strong enough to be labeled "approximately invariant". Charnov (1993) has developed a model to account for them in which

adult mortality rates set the tradeoffs that determine optimal age at maturity. Annual fecundity varies with both. Though very simple, the model also captures and accounts for important differences between primates and other mammals (Charnov & Berrigan, 1993).

If the grandmother hypothesis explains extended human lifespans, and if human life histories maintain the broad patterning apparent across primates, then other human life history traits should be adjusted to predictable values relative to those observed in other living hominoids. Specifically, age at maturity should be delayed as a function of reduced adult mortality rates, but instead of the lower annual fecundity that normally goes with later age at maturity in other primates, grandmother's help pays off in higher fertility. Comparison of averages for modern human foragers and wild populations of chimpanzees, gorillas, and orangutans yields results consistent with these expectations (Hawkes *et al.*, 1998a). Not only do we have longer lifespans, but, as predicted by the combination of the grandmother hypothesis and Charnov's life history model, we also mature later and produce offspring at a higher rate.

#### *An evolutionary scenario*

Our analysis of Hadza women's foraging and food sharing leads us to propose a set of closely related hypotheses about the evolution of these distinctive features of human life history (Hawkes *et al.*, 1997, 1998a,b). Imagine an ancestral hominid with life history characteristics and foraging patterns comparable to those of the modern chimpanzee. In particular (and unlike modern humans), age at maturity was about 10–12 years and fecundity was relatively low. Children were sometimes fed by mothers and older siblings, particularly with items they themselves could not handle, but the overall importance of these foods was marginal.

The fertility of older females declined sharply in tandem with other aspects of physiology; maximum lifespan was about 50 years.

Imagine further a significant change in environment that reduced the availability of resources that younger juveniles could take on their own. Under these circumstances, local populations might have adjusted their foraging ranges, perhaps abandoning some areas entirely. Alternatively, they might have invested more in provisioning, especially with resources that may have been avoided before because although adults could handle them effectively, young children could not. For the strategy to be effective, returns must have been high enough to support the collector and at least one other individual. They must also have been available on a daily basis, with relatively low variance in returns between collecting bouts. Otherwise, their utility to small, growing youngsters would have been limited.

As provisioning became established, older females who were slightly more vigorous, despite declining fertility, could have assisted in the process, enhancing the survivorship of youngsters they helped while allowing the mothers of those offspring to begin a new pregnancy sooner. Less vigorous menopausal females would have provided less help. Higher reproductive success for the junior kin of more vigorous older females would have reduced the relative frequency of deleterious alleles expressed around menopause. Higher reproductive success for young adults with older helpers would also alter the tradeoffs between allocation to current reproduction in early adulthood versus allocation to maintenance for later adaptive performance. The help of vigorous oldsters could more than compensate for reduced allocation to current reproduction by the junior kin themselves. Selection against senescence would be strengthened by both these pathways, decreasing adult mortality rates so that more

would live to peri-menopausal, then post-menopausal ages. Longer adult lifespans would in turn have an effect on age at maturity. Lower adult mortalities increase the likelihood of reproducing before dying. Consistent with general mammalian (including primate) patterns (Charnov, 1993), delayed maturity, a longer period of growth, larger adult body size, and later age at maturity would have followed as a result. Extended fertility would *not* have been favored as it would have interfered with assistance to grandchildren and the enhanced fecundity at younger ages enjoyed by the daughters of older helpers. Instead, a fertile span similar to that of the other apes would have been conserved, the derived feature being extended post-menopausal longevity.

Increased offspring provisioning and related changes in fitness would also have had important ecological implications (Hawkes *et al.*, 1997, 1998b). High juvenile mortality rates in modern primates are often attributable to feeding competition (van Schaik, 1989). If this were the case in the ancestral hominid population, then any increase in offspring provisioning should have reduced juvenile mortality. If the resources involved occurred in dense patches, with returns limited by handling requirements rather than by abundance, then their use should also have allowed the formation of larger foraging groups (Janson & Goldsmith, 1995; Wrangham *et al.*, 1993). These would have been strongly favored by the requirements that grandmothers be near enough to daughters and grandchildren to support them. Where juvenile foraging capabilities previously limited habitat use, sharp increases in geographical range should also have been facilitated. To the degree that handling costs constrained adult returns from newly adopted resources, innovations in handling efficiency, including new technology, should also have been favored (Hawkes & O'Connell, 1992).

### Applying the argument to *Homo erectus*

Pursuing this hypothesis into the fossil and archaeological record has so far involved five steps: (1) marking the points in the hominid past at which life history changes are indicated, (2) examining the fit between changes inferred by paleoanthropologists and those predicted by the grandmother hypothesis in combination with Charnov's life history model; (3) assessing the evidence for coincident changes in climate and environment that might have reduced access to "children's" resources; (4) nominating resources previously unused but likely to have been adopted in response to these changes; (5) assessing the evidence that these resources were actually exploited more heavily coincident with changes in climate and hominid life history.

#### *Homo erectus* life history

Significant changes in hominid life history are currently identified at two, possibly three points in the fossil record, one associated with the appearance of *H. erectus*, another with archaic *H. sapiens*, a third (least certainly, see below) with fully modern humans (Smith & Tompkins, 1995). Here we are concerned only with those changes associated with *H. erectus*. The appearance of this form is marked by shifts in brain size, dental eruption schedules and adult body weight, all read to indicate increased longevity and delayed maturity. Age at weaning should also have been adjusted, though the data needed to test this prediction have yet to be assessed:

- Estimates of longevity in fossil taxa are based on the correlation between brain size and longevity in living primates, including modern humans (Austad & Fisher, 1992; Sacher, 1959). Australopithecine brains were about the same size as those of modern chimpanzees (400–500 cc), suggesting similar adult mortality rates and, by this index,

lifespans of about 50 years. Modern humans, with brain sizes of 1100–1700 cc, have much lower adult mortalities, with maximum lifespans estimated at 90–100 years. Brain sizes in *H. erectus* range from about 800–1100 cc, intermediate between values for australopithecines and modern humans, indicating similarly intermediate rates of adult mortality, and so intermediate maximum lifespans (Sacher, 1975).

- Dental eruption schedules provide an index of age at maturity (e.g., Beynon & Dean, 1988; Bromage & Dean, 1985; Smith, 1986, 1989, 1993). In australopithecines, M1, an important developmental marker closely correlated with other features of life history, including age at maturity, erupted at about age 3–3.5 years, the same age as in chimpanzees, but short of the 5.5–6 year figure for modern humans. In *H. erectus*, age at M1 eruption is estimated at about 4.5 years. These data suggest that australopithecines matured at about age 10, as do modern chimps, while *H. erectus* reached that threshold at about age 15.
- Adult body size is also an index of age at maturity. In Charnov's life history model, reduced adult mortality favors growing longer before switching production from growth into offspring. Maternal size is thus expected to increase with delayed maturity. Estimates of fossil hominid body weight are based on various post-cranial indicators, notably the correlation between femoral head diameter and body weight in modern humans. This relationship suggests average adult weights of 35–40 kg for australopithecines, 55–60 kg for *H. erectus*, an increase of about 55% (McHenry, 1994; Ruff & Walker, 1993). The difference across females is especially striking: 30–35 kg for australopithecines, 50–55 kg for *H. erectus*, an increase of roughly 70%.
- Age at weaning in *H. erectus* should be no later than in apes and australopithecines.

Although in mammals later age at maturity is usually correlated with lower annual fecundity, grandmothing raises the rate of baby production. Shorter interbirth intervals should be indicated by age at weaning, which in turn should be marked by changes in the chemical composition of permanent teeth that formed across the weaning period, specifically by lower post-weaning values for O<sup>18</sup>, N<sup>15</sup> and Sr/Ca, and higher values for C<sup>13</sup>, all associated with the shift in trophic level and the adoption of solid foods (e.g., Wright & Schwarcz, 1998). It may also be indicated by an increase in the incidence of stress-related enamel hypoplasia (e.g., Goodman *et al.*, 1984; cf. Hillson & Bond, 1997). These changes can be tracked relative to crown formation schedules (e.g., Wright & Schwarcz, 1998), or on the incremental growth features of individual teeth (Cerling & Sharp, 1996), both of which may in future allow estimates of age at weaning in *H. erectus*.

On the basis of general correlations, available brain and body weight and dental eruption data, though limited, can be read to indicate that longevity was increased and maturity delayed in *H. erectus* relative to the broader hominoid (including earlier hominid) pattern. In australopithecines, values for both were apparently similar to those in modern chimpanzees; in *H. erectus*, intermediate between those of australopithecines and modern humans.<sup>4</sup> Our model assumes

<sup>4</sup>On brain and body weight criteria (e.g., McHenry, 1994), it might be argued that *H. habilis*, not *H. erectus*, is the earliest hominid to display distinctively non-pongid life history characteristics. Attempts to confirm this through analysis of dental eruption schedules have so far proven inconclusive (e.g., Dean, 1995; B. H. Smith, 1991; R. J. Smith *et al.*, 1995). The issue is complicated by small sample size and continuing uncertainty about the taxonomy of key specimens (e.g., White, 1995). Even if *H. habilis* life history differed from the general hominoid pattern, available data indicate that *H. erectus* marked a more pronounced departure.

that the length of the fertile period did not differ between *H. erectus* and australopithecines. This is difficult to assess in the fossil record, but given the apparent conservativeness of this attribute [fertile periods in chimpanzees and humans are essentially the same (Hill & Hurtado, 1996:463; Schultz, 1969)], it seems simplest to assume the same period for all ancestral hominids, including *H. erectus*.

#### *Climate change and "children's" resources*

Our hypothesis leads us to expect that life history changes in *H. erectus* were prompted by a decline in the availability of resources easily taken by children (e.g., fruit). Generally speaking, such declines should have been associated with shifts toward cooler, drier, more seasonal climates. In tropical Africa, cooler, drier winters would have been especially critical. Plant foods accessible to humans are very limited in this season. Those that are available (e.g., seeds, nuts, underground storage organs) typically have relatively heavy handling costs (Peters & O'Brien, 1981; Peters *et al.*, 1984).

Data from deep marine sediments indicate a general trend toward cooler climates world-wide over the past three million years, with marked steps in this direction at 2.8–2.5, 1.9–1.7, and 0.9–0.8 Ma (e.g., deMenocal, 1995). Terrestrial data (e.g., soil chemistry, pollen, fossil faunas) show progressive increases in aridity and seasonality and related expansion of open habitats in tropical Africa from 2.5–1.7 Ma (Behrensmeyer *et al.*, 1997; Cerling, 1992; Cerling *et al.*, 1988; Reed, 1997; Spencer, 1997; Vrba *et al.*, 1995). These changes were evidently reinforced by continental uplift (Partridge *et al.*, 1995), and a long term trend toward lower levels of atmospheric CO<sub>2</sub> (e.g., Street-Perrott *et al.*, 1997).

At least three lines of evidence mark the 1.9–1.7 Ma period bracketing the earliest

dates for African *H. erectus* (Feibel *et al.*, 1989; White, 1995) as especially critical from the perspective of our model:

- Soil carbonates indicate a sharp increase in the abundance of C4 biomass (an index of aridity and seasonality) in both the Turkana and Olduvai regions at about this time (Cerling, 1992). Prior to ca. 1.7 Ma, neither area had more than about 50% C4 biomass present; thereafter values jump to 60–80%.
- Feeding and habitat preferences of animals represented in early East African hominid sites show a complementary trend: arboreal and (more notably here) frugivorous animals formerly common in these localities are much less so after 1.8 Ma (Reed, 1997).
- Indicators of seasonal dietary stress are common in the teeth of fossil theropitths from Koobi Fora after 2.0 Ma (Macho *et al.*, 1996).

#### *"Tubers" as the newly exploited resource*

Resources adopted to provision juveniles in response to these changes must have been: (1) generally available, especially in the dry season, (2) capable of yielding returns high enough to support the collector and at least one other person, (3) reliable enough to provide those returns with little or no daily variance, and (4) open to exploitation by adults but not younger children. Many resources meet these criteria, notably certain varieties of small game, shellfish, nuts, seeds and the underground storage organs of plants. Here we restrict our attention to underground storage organs (hereafter "USOs" or, loosely, "tubers"), primarily because their availability and exploitation costs are relatively well understood, and because it has often been suggested that tubers were important in early hominid diets (e.g., Hatley & Kappelman, 1980; Isaac, 1980; McGrew, 1992; Peters & O'Brien, 1981; Stahl, 1984; Vincent, 1985a,b).

Parallel treatment of other potential provisioning resources is clearly in order.<sup>5</sup>

USOs store water and carbohydrates (e.g., Anderson, 1987; Chapin *et al.*, 1990). They take many forms, including bulbs, corms, rhizomes, taproots, tubers, and woody rootstocks, and are especially well-represented among the Liliaceae, Dioscoreaceae, Araceae, Taccaceae, and Icacinaeae (Raunkiaer, 1934; Thoms, 1989). Consistent with function, they are common in seasonally dry and/or cold habitats, often representing up to 20% of local species, sometimes occurring at densities of more than 1000 kg/hectare (e.g., Thoms, 1989; Vincent, 1985*b*). Edible carbohydrate content varies but generally represents 50–90% of dry weight in most species.

Wild forms are heavily exploited by modern humans in tropical through cool temperate latitudes on all continents (e.g., Bahuchet *et al.*, 1991; Coursey, 1967; Endicott & Bellwood, 1991; Gott, 1982; Hladik & Dounias, 1993; Hurtado & Hill, 1990; Johns, 1990; Lee, 1979; Malaisse & Parent, 1985; O'Connell *et al.*, 1983; Thoms, 1989; Turner & Davis, 1993; Vainshtein, 1980; Vincent, 1985*a,b*; Watanabe, 1973). By contrast, they are rarely eaten by other primates except in arid, highly seasonal habitats, and even then only if they are found close to the ground surface (McGrew, 1992; McGrew *et al.*, 1988; Moore, 1992; Peters & O'Brien, 1981; Whiten *et al.*, 1992).

Although attractive as a potential energy source, tubers can present certain problems to human consumers: they may be heavily defended, either mechanically or chemically (Anderson, 1987; Coursey, 1973), and their carbohydrate content may be difficult to

digest without pre-consumption processing (Thoms, 1989; Wandsnider, 1997). Mechanical defenses can often be countered by simple technology (e.g., digging sticks), chemical ones by a variety of techniques including maceration, leaching, boiling, baking, or roasting (Johns & Kubo, 1988; Lancaster *et al.*, 1982; Spenneman, 1994; Stahl, 1984; Wandsnider, 1997).

Cooking also has an important effect on digestibility. The principle storage carbohydrates in tubers are starch, sucrose, and fructan (Banks & Greenwood, 1975; French, 1973; Lewis, 1984; Macdonald, 1980). Each occurs in a variety of molecular forms. Simpler types are water-soluble and easily handled raw by human digestive systems, though cooking usually improves nutrient yield. More complex forms definitely require cooking (French, 1973; Gaillard, 1987; Macdonald, 1980; Stahl, 1984; Wandsnider, 1997). Cooking also softens structural cellulose, which reduces intestinal "hurry", the speed with which high-fiber foods otherwise move through the gut. Slower passage generally increases nutrient yield (Macdonald, 1980; Stahl, 1984).

Two USOs favored by Native Americans, biscuit root (*Lomatium cous*) and camas (*Camassia quamash*), illustrate the effect of carbohydrate form on processing requirements. The primary storage medium in biscuit root is starch (dry weight fraction 40%; Yanovsky & Kingsbury, 1938). Under traditional conditions, this tuber was eaten raw, dried, or lightly boiled. It was also occasionally ground into flour and pressed into small cakes (Couture, 1978). No roasting or other extensive cooking was required. In contrast, the principal storage carbohydrate in camas is inulin (35–45% dry weight), a molecularly complex form of fructan only marginally digestible in raw form by humans. Traditional processing involved steaming the roots for 24–72 h in large rock-lined earth ovens, hydrolyzing

<sup>5</sup>For data on age-related handling costs and nutrient returns for other potential provisioning resources, see (for example) Blurton Jones *et al.* (1994*a,b*), Boesch & Boesch (1984) and Peters (1987) on nuts, Bird & Bliege Bird (1997), Bliege Bird *et al.* (1995), and Meehan (1982) on shellfish.

**Table 1** Some post-encounter return rates from wild tubers

Location	Resource	Type	Return (kcal/hr)
Central Australia	<i>Cyperus</i> sp.	Corm	≥4500 <sup>1</sup>
	<i>Ipomoea costata</i>	Rhizome*	6200 <sup>1</sup>
	<i>Vigna lanceolata</i>	Rootstock	1700 <sup>1</sup>
East Africa	<i>Vigna frutescens</i>	Rootstock*	1000–3500 <sup>2,3</sup>
	<i>V. macrorhyncha</i>	Rootstock*	3000 <sup>2</sup>
	<i>Vigna</i> sp.	Rootstock*	900 <sup>2</sup>
	<i>Vatovaea pseudolablab</i>	Rootstock*	2000 <sup>2</sup>
South Africa	<i>Coccinea rehmannii</i>	Rootstock*	2900 <sup>4</sup>
	<i>Vigna dileri</i>	Rootstock	3000 <sup>4</sup>
	<i>Camassia quamash</i>	Bulb*	2000–4000 <sup>5</sup>
Western North America	<i>Lomatium</i> spp.	Rootstock	1000–4000 <sup>6</sup>
	<i>Lewisia rediviviva</i>	Rootstock*	1200–1400 <sup>6,7</sup>

\*Item requires roasting, baking, or boiling.

<sup>1</sup>O'Connell & Hawkes, 1981; O'Connell *et al.*, 1983.

<sup>2</sup>Vincent, 1985*a,b*.

<sup>3</sup>Hawkes *et al.*, 1995.

<sup>4</sup>Blurton Jones *et al.*, 1994*b*.

<sup>5</sup>Thoms, 1989.

<sup>6</sup>Couture, 1978; Couture *et al.*, 1986.

<sup>7</sup>Simms, 1987.

the fructan to easily digested fructose (Konlande & Robson, 1972; Thoms, 1989). (See also Gott, 1983; Incoll *et al.*, 1989; Turner & Kuhnlein, 1983; Turner *et al.*, 1992; Wandsnider, 1997 for additional examples.)

The difficulties of coping with USO defenses and managing any required cooking are probably great enough to prevent pre-adolescent human children from exploiting many, perhaps most, USOs effectively. In the Hadza case, children as young as five often take shallow-growing *makalita* (*Eminia antenulifera*), but cannot cook the starchy, fibrous roots for themselves if fire kindled by an elder is unavailable. Thus, their returns may often be relatively low. The hard, sustained effort entailed in acquiring deeply buried *llekwa* (the tuber favored by adults) prevents even older children from digging it efficiently, long after they can handle the necessary roasting.

These difficulties also constrain tuber use in chimpanzees. McGrew (1992:146) observes that the only USOs exploited by chimps are “either small bulbs simply pulled

up by hand or surface roots directly gnawed”. Though chimpanzees can make simple tools that might be suitable for collecting deeply buried tubers, and in some circumstances are even able to maintain fire [e.g., in connection with cigarette smoking (Brink, 1957)], they apparently never use either skill to take tubers in the wild, probably because other resources, easily taken by juveniles, are readily available in the habitats they occupy.

Quantitative data on return rates from wild tuber collecting are limited, but sufficient to show that they are often high enough to support the collector and one or more dependents, even where significant processing is required (Table 1). Values for a sample of tropical African and Australian and temperate North American forms range from 1000–6000 kcal/h (in patch). Assuming collectors spend about 4–6 h/day at the task (e.g., Hawkes *et al.*, 1997; Thoms, 1989), daily returns from these resources would vary from roughly 4000–36,000 kcal/collector. Short-term variance in the best-controlled case (Hawkes *et al.*, 1989, 1995)

is low,  $\ll 50\%$ .<sup>6</sup> Observations among the Hadza, !Kung and Australian Alyawarra (Blurton Jones *et al.*, 1994a,b; Hawkes *et al.*, 1989, 1995; O'Connell *et al.*, 1993) indicate that returns of 8000–12,000 kcal/collector-day may be common in tropical savanna habitats. Thoms' (1989) summary of historical data on various Columbia Plateau groups suggests that in cool temperate steppe situations returns may be 2–3 times that high. Because tubers often occur at relatively high densities, such returns can be sustained for long periods of time (weeks or months) within daily foraging distance of a single residential base, even under intense collecting pressure (Hawkes *et al.*, 1989, 1997; Thoms, 1989; Vincent, 1985a,b). Heavy culling may actually improve return rates in successive seasons (e.g., Anderson, 1987; Gott, 1983; Thoms, 1989).

The potential importance of tubers to ancestral hominids, specifically *H. erectus*, depended in part on their availability. Two lines of evidence point to greater abundance over the last 2.5 Ma, and especially after 1.8 Ma. One is overall pattern of tuber density in modern habitats. Surveys of African tropical forest communities show that tubers useful to humans are present at densities of about 1–10 kg/hectare (Hladik & Dounias, 1993). Similar assessments in African savanna and North American steppe situations indicate values in the range 1–100 T/hectare, up to five orders of magnitude higher (Thoms, 1989; Vincent, 1985a,b). Since these and other open habitats have become more common over the past 2–3 Ma, it seems reasonable to think that tuber abundance, diversity and distribution have increased accordingly, particularly after 1.8 Ma. The African paleontological record provides striking confirmation: suids, which

rely heavily on USOs as a food resource, show a sharp increase in taxonomic diversity at ca. 1.8 Ma (White, 1995).

*Archaeological and fossil evidence for tuber use*  
Archaeological evidence of tuber exploitation is often limited and indirect. Nevertheless, we can identify at least four patterns in the record consistent with the use of USOs beginning with the appearance of *H. erectus*:

- *Geographical range.* Prior to ca. 1.8 Ma, hominids were confined to relatively well-watered parts of tropical and subtropical Africa (Reed, 1997). *H. erectus* was far more widespread, both within Africa and beyond, though never further north than about latitude 45–50 degrees (Dennell & Roebroeks, 1996; Gabunia & Vekua, 1995; Gibert *et al.*, 1998; Roebroeks *et al.*, 1992). Though the increase in range is often read to mean heavy reliance on hunting, this was unlikely to have been a productive strategy in many of the habitats newly occupied, particularly the more arid ones. Large animal biomass is typically low in such settings, implying high variance and low reliability in prey acquisition rates. USOs would have been much more dependable targets. Interestingly, latitude 50 marks not only the northern boundary of *H. erectus*, but also the approximate limit of reliance on tubers as a staple among ethnographically known hunter-gatherers in continental habitats (Thoms, 1989).<sup>7</sup>

<sup>7</sup>An extensive literature review leads Thoms (1989:94) to observe: "Although there is considerable variation in the use of geophytes across [northern Eurasia], the overall pattern is one of minor use in the tundra and the northern part of the taiga zone, moderate use in the taiga zone, and comparatively heavy use along the southern margins of the taiga and the northern part of the steppe." The same review indicates a similar pattern in western North America. In both cases, the steppe/forest boundary falls at about latitude 50 degrees. Clearly, it would be useful to know more about the determinants of this pattern, as well as about whether and in what ways they may have limited the distribution of *H. erectus* in the past.

<sup>6</sup>Most of the return rate variance indicated for this case probably reflects differences in collector effort, not encounter rate. It is our impression that day-to-day variance in return rates for older women is very low, perhaps negligible.

- *Digging tools.* Shallow-growing USOs can often be gathered by hand, but efficient acquisition of deeply buried forms requires, at minimum, a digging tool. Nearly a dozen pointed long-bone fragments, all showing damage to the tip said to be consistent with such use, are reported from Member 1 at Swartkrans Cave, dated at about 1.7 Ma (Brain, 1988). Stone tools suitable for the manufacture of wooden digging sticks (unifacial choppers and heavy scrapers) are common in the Oldowan Industry, which dates to ca. 2.5 Ma (Harris, 1983; Harris *et al.*, 1987; Howell *et al.*, 1987), but is especially well-known and widely encountered after 2.0 Ma (Isaac & Harris, 1978; Leakey, 1971). Keeley & Toth (1981) report damage consistent with woodworking on at least some early specimens. Later Acheulean and so-called “chopper-chopping tool” industries also include implements applicable to this task.
  - *Evidence of fire.* Some tubers may be eaten without preparation, but, as noted above, cooking typically improves the nutritional yield of even the simplest starches. Where storage carbohydrates are more complex and/or chemically defended, cooking is essential. Where cooking is practised, the likelihood of encountering archaeological evidence depends on the particular techniques employed. Some will be obvious [e.g., rock-filled earth ovens used in connection with camas processing (Thoms, 1989)]; others less so. Among the Hadza, for example, *//ekwa* roots are typically roasted for 5–15 min in large fires kindled on unprepared ground surfaces. Even where cooking sites are used repeatedly, archaeological evidence of this practice is likely to be ephemeral. The earliest unambiguous evidence for the use of fire by humans dates to the late Middle Pleistocene, 250–400 ka (Clark & Harris, 1985; James, 1989). Earlier indications include burned animal bones from Swartkrans, dated 1.0–1.5 Ma (Brain & Sillen, 1988), and small patches of reddened earth associated with stone tools and large animals bones at Chesowanja and East Turkana, dated 1.4–1.6 Ma (Bellomo, 1994; Gowlett *et al.*, 1981; Isaac & Harris, 1978). Fire is indicated in all three cases; the question is whether hominids, specifically *H. erectus*, were involved in creating or maintaining it. In at least the eastern African cases, the associations with stone tools might be read to suggest that they were.
  - *H. erectus digestive anatomy.* Milton & Demment (1988) report that modern human digestive tracts are smaller, relative to body size, than those of chimpanzees, probably as a function of differences in diet. The foods humans eat generally require less digestive processing than those favored by chimpanzees, partly because of pre-consumption processing, including cooking. Aiello & Wheeler (1995) argue on grounds of thoracic morphology that modern (or near-modern) human digestive systems first appeared with *H. erectus*. Earlier hominids display the funnel-shaped thorax typical of modern chimpanzees; *H. erectus* and later *H. sapiens* fossils all show the barrel shape found in modern humans. If Aiello and Wheeler are right, then beginning with *H. erectus*, humans either (1) narrowed the range of resources commonly exploited, focusing on those most readily digested, or (2) invested more effort in pre-consumption processing as means of reducing digestive costs. Tuber cooking is a good example of the latter strategy.
- We can also point to at least two other potential tests for the importance of tubers in *H. erectus* diets. One involves analyses of dentition. Suwa *et al.* (1996) summarize evidence for reduced molar surface areas in

early *H. erectus* relative to australopithecines, a pattern consistent with the idea of higher food quality and/or increased pre-consumption food processing just described. If tuber consumption produces distinctive damage patterns on teeth, then it might be implicated in these changes by inspection of the teeth in question.

The second test involves trace element analysis. Sillen & Lee-Thorp (1994) review research indicating differential concentration of strontium relative to calcium in plant storage organs, and discrimination against strontium across trophic levels. They further report that dietary fiber binds calcium more effectively than it does strontium; thus, all else equal, high-fiber eaters should display higher skeletal Sr/Ca than low-fiber eaters. These observations collectively suggest that if *H. erectus* relied heavily on tubers, their skeletons should display relatively high Sr/Ca ratios. If, on the other hand, and as generally believed, meat was the critical new element in *H. erectus* diets, their skeletal Sr/Ca ratios should be relatively low.

*An evolutionary scenario grounded in the Plio-Pleistocene*

Data on *H. erectus* life history, climate, and resource use developed and integrated so far can be summarized along the following lines. By ca. 1.8 Ma, a long-term trend toward cooler, drier climate led to sharp reductions, at least seasonally, in the availability of plant foods previously exploited by hominids, especially juveniles. In some populations, adults and older juveniles increased a previously infrequent practice of using resources that younger children could not acquire on their own, with mothers and older siblings providing shares to the younger ones. Without weanlings of their own, aging females were able to feed their daughter's youngsters. Those more vigorous could support a weanling fully, allowing their daughters to wean early and begin their

next pregnancies sooner, with less impact on their weanlings' welfare. This increased selection against senescence, thereby lowering adult mortality rates and in turn favoring later maturity. Extended lifespans did not favor delaying menopause since females who continued to have babies of their own were unable to enhance their daughters' fertility. Lineages with higher fertility rates were those with post-menopausal helpers. Relaxation of the limits previously imposed on adult foraging by children's resource handling capabilities opened a broader range of habitats to exploitation. Longer-lived, and so later-maturing, larger-bodied, bigger-brained hominids, identifiable as *H. erectus*, quickly spread throughout the Old World tropics and into temperate latitudes.

Tubers may have been among the newly or increasingly used resources that enabled these changes. The same shift toward more open habitats that probably reduced access to "children's" foods almost certainly increased the availability of USOs. Whether they were exploited and, if so, how effectively depended on the handling problems they posed, and on the technology available to cope with them. Digging sticks could have been fashioned with then-extant stone tools and used to exploit deeply buried but chemically-undefended tubers, particularly those with simpler forms of carbohydrate storage. If fire could be made on demand, or at least maintained once "captured", then chemically more challenging forms might also have been accessible. If not, the returns potentially available from USOs, the advantages associated with provisioning, and related adjustments in life history would have been constrained accordingly. Apparent changes in hominid gut anatomy and evidence for fire at Lower Pleistocene sites might be read to indicate that tubers were cooked and consumed extensively. If so, they may well have played a critical role in the emergence and subsequent evolutionary success of *Homo erectus*.

## Discussion

Although this argument raises a wide range of issues, we comment here on just three: (1) a likely objection to the notion of long lifespans for *H. erectus*, (2) the implications of the grandmother hypothesis for current ideas about early human social organization, and (3) the importance of meat-eating in early human evolution.

### *Long lifespans among pre-modern humans*

As applied to *H. erectus*, our model runs counter to the notion, widely held in some quarters, that long post-menopausal lifespans are a recent phenomenon, possibly the product of advances in medicine and basic sanitation made just in the last century or so, but definitely dating no earlier than the appearance of modern *H. sapiens* sometime in the early Upper Pleistocene (50–100 ka). There are good reasons to be skeptical of this proposition.

The idea that long lifespans are a very recent development stems at least in part from confusion over the implications of well-documented changes in *average life expectancy at birth*. This has increased substantially in some contemporary populations, largely due to sharp drops in infant and juvenile mortality rates. Low survivorship in the early years has a large effect on average lifespans. If, for example, half of those born die in the first year of life while everyone else lives to 100, life expectancy at birth must be near 50, even though all adults live well past that age. As it happens, old people, at least in their late 70s, are encountered everywhere, even in small populations, far from scientific medical care. Among the Ache, !Kung and Hadza, for example, average life expectancy at birth is about 35 years, yet average female life expectancy at age 45 is about 20 additional years (Blurton Jones *et al.*, 1992; Hill & Hurtado, 1996; Howell, 1979). Again, this is an average: many live much longer. In all these cases, nearly 40% of adult women are post-menopausal.

The notion that long lifespans are restricted to modern *H. sapiens* is based on the fact that individuals identified as “old” (aged  $\geq 50$  yrs) are uncommon in the fossil record. Trinkaus (1995) and others appeal to a variety of skeletal indicators (e.g., epiphyseal fusion, dental attrition, and long bone histomorphometry) in arguing that archaic *sapiens* routinely sustained high mortalities in young adulthood and seldom lived past age forty (see also Abbott *et al.*, 1996; Bermudez de Castro & Nicolas, 1997). Though comparable analyses have yet to be undertaken on *H. erectus*, a similar argument might well be anticipated: long post-reproductive lifespans, predictable in theory, were seldom if ever actually achieved.

There are two important problems with this argument, either as applied to archaic *H. sapiens* or anticipated with respect to *H. erectus*:

- Older adults will *always* be under-represented in archaeological samples, simply because their remains are more susceptible to decay due to bone mineral depletion (e.g., Buikstra & Konigsberg, 1985; Galloway *et al.*, 1997). The absence of elderly individuals in excavated cemetery populations of which they are *known*, on the basis of historical records, to have once been a part, illustrates the effect (e.g., Walker *et al.*, 1988).
- Skeletally-based age estimates on adults over age 25 are notoriously inaccurate and commonly underestimate true age, sometimes by decades (e.g., Aiello & Molleson, 1992; Bocquet-Appel & Masset, 1982, 1996; Jackes, 1992; Konigsberg & Frankenberg, 1992; Paine, 1997).

Failure to appreciate the pervasive effects of these factors has sometimes led analysts to infer high young adult mortality rates and short lifespans even for modern human populations known archaeologically (e.g., Lovejoy *et al.*, 1977). It is now generally

recognized that such inferences are inappropriate (Aiello & Molleson, 1992; Bocquet-Appel & Masset, 1982, 1996; Howell, 1982; Jackes, 1992; Konigsberg & Frankenberg, 1992; Paine, 1997). Similar arguments about earlier hominid mortality and lifespan should be treated with equal skepticism.

Correlations between brain weight, maximum lifespan, and age at maturity documented across the primates (e.g., Austad & Fisher, 1992; Sacher, 1975) lead us to expect that long lifespans and late maturity have been typical of most humans since the late Middle Pleistocene (200–500 ka), when brain sizes in archaic *H. sapiens* reached the modern range (Leigh, 1992; Ruff *et al.*, 1997). Though skeletal data enabling estimates of age at maturity in early *H. sapiens* are limited, the few available are consistent with the idea that this threshold was achieved late, at roughly the same age as in modern humans (e.g., Dean *et al.*, 1986; Mann & Vandermeersch, 1997; Stringer & Dean, 1997; Stringer *et al.*, 1990; Tompkins, 1996). The same reasoning leads us to expect earlier increases in average adult lifespan and age at maturity, beyond the hominoid range but short of those associated with *H. sapiens*, coincident with the first appearance of *H. erectus*. As indicated above, data on brain size, dental eruption schedules, and body weight are all consistent with this proposition.

#### *Implications for H. erectus social organization*

The grandmother hypothesis has important implications for current opinion about hominid social organization; in particular, for the suggestion, commonly made (e.g., Foley & Lee, 1989; Ghiglieri, 1987; Rodseth *et al.*, 1991; Wrangham, 1987) and now widely echoed (e.g., Mellars, 1996), that evidence of male philopatry and female dispersal among chimpanzees and modern human hunter-gatherers implies that both were characteristic of *all* ancestral hominids,

including *H. erectus*. Elsewhere (Hawkes *et al.*, 1997), we have detailed reasons to be skeptical of this suggestion; among them, that patterns of residence, alliance, and dispersal vary widely among both chimps and modern hunters, and that all are evidently sensitive to local ecological conditions, especially as they affect female subsistence.

The grandmother hypothesis allows us to build on these observations more pointedly, specifically with reference to *H. erectus* social organization. Heavy reliance on high cost/high yield resources in connection with offspring provisioning should have given daughters a strong incentive to remain with their natal group. As daughters grew, they acquired the strength and skill needed to feed younger siblings. When they matured, the assistance of aging mothers continued to enhance the benefits of proximity. From this perspective, long post-menopausal lifespans, late age at maturity, and high fertility suggest a pattern of co-residence among related females. The stronger the pattern, the greater the incentive for males to leave their natal group.

Grandmothers could certainly have improved their fitness by aiding sons, but the benefits associated with helping daughters are likely to have been much greater. Mothers and daughters face similar reproductive tradeoffs: both do better by attending to offspring survivorship. Sons generally do better by investing in mating (Anderson, 1994; Hawkes *et al.*, 1995). A food-sharing mother might attract females to her son's group, but this would not assure her son paternity of those females' offspring. His fitness would depend on his success in competing with other males. Winners of that competition would enjoy higher reproductive success whether or not their mothers contributed to the fertility of their mates. Even if a grandmother could identify her son's offspring and single out grandchildren to feed, her potential fitness gains through increased fertility of "daughters-in-law"

would be devalued by the uncertain paternity of subsequent children more quickly born to the mother of those grandchildren.

*What about the archaeological evidence for big game hunting and scavenging?*

This brings us a third issue, the common association between stone tools and the remains of large animals at sites of Lower and early Middle Pleistocene age that many continue to see as strong support for the hunting hypothesis. Though comprehensive consideration of these remains is well beyond us here, a brief comment grounded on our general argument seems pertinent.

As indicated above, heavy reliance on resources like tubers that occur at high densities, with returns limited primarily by handling requirements, should have favored larger group sizes. The associated predator-defense advantages should have reinforced the pattern, especially in more open habitats. Along with larger body size, larger group size should also have provided an important edge in "aggressive" or "confrontational" scavenging, where the kill is seized from the initial predator while still substantially intact (O'Connell *et al.*, 1988b). Increased consumption of meat and marrow, and correspondingly increased evidence of such consumption in the archaeological record, should have been among the outcomes. There is little indication of meat consumption by hominids in the late Pliocene (Kibunjia, 1994). Instead, the earliest sites implicated in recent arguments about the hunting hypothesis date to the Plio-Pleistocene boundary (e.g., Bunn, 1994; Bunn & Kroll, 1986), coincident with the first evidence for African *H. erectus*. Recent analyses of cut- and tooth-mark distribution in the assemblage from the well-known "Zinjanthropus" site at Olduvai (Capaldo, 1997; Dominguez-Rodrigo, 1997) suggest that the sequence of carcass access there may have been carnivore-hominid-carnivore, consistent with the

notion that hominids were successful in aggressive confrontations over large animal carcasses killed by other predators.

Success at acquiring carcasses need not have implied restricted mating access ("pair bonding") or paternal provisioning, any more than it does among chimpanzees. Neither would transport of parts to "central places" be indicated (cf. Bunn & Ezzo, 1993; Potts, 1988; Rose & Marshall, 1996): individuals or groups may simply have called attention to any carcass they encountered or acquired, just as do modern human hunters (O'Connell *et al.*, 1988a,b, 1992). If the carcass had not yet been taken, the crowd so drawn could have done so, then consumed it on or near the spot, again just as modern hunters sometimes do (O'Connell *et al.*, 1988b). The same advantages that helped secure the carcass initially—large body size and large group size—would often have deterred any counter-attack, either by the original predators or others arriving later. Repeated successes at the same spot, perhaps a dry season water source in a stream channel, would create archaeological sites very like those often identified as characteristic of the Lower Pleistocene record, particularly in East Africa. Subsequent density-dependent attrition of the bone assemblage would have sealed the match (Marean *et al.*, 1992). Archaeological visibility notwithstanding, the sites so created need not indicate that large animal prey were either commonly acquired or an important part of *H. erectus* diets. On the contrary, their appearance might simply reflect changes in hominid group and body size stimulated largely if not entirely by prior changes in female foraging, food sharing, and life history.

### Summary

Clear-cut, probably widespread patterns in women's foraging and food sharing among modern tropical hunter-gatherers have an

important effect on children's nutritional welfare. This observation is the basis for an hypothesis about the evolution of extended lifespans typical of all living humans. Because elements of mammalian life histories vary with each other systematically, other aspects of ancestral hominid life histories should have been entrained simultaneously. Longer adult lifespans favored by the payoffs for grandmothering when mothers provision their offspring should account for the delayed maturity, relatively high fertility and mid-life menopause that collectively distinguish humans from other living hominoids. Here we have used this foundation to develop a scenario for the evolution of *Homo erectus*; then assessed it in light of the available data on *H. erectus* life history and anatomy, Plio-Pleistocene environment, the economics of tuber exploitation, and Lower Paleolithic archaeology. Results show that these lines of evidence are consistent with the proposition that grandmothering played a central role in the evolution and spread of this long successful taxon. Widely held ideas about the recent development of long human lifespans, the prevalence of male philopatry among ancestral hominids, and the catalytic role of hunting and scavenging in early human evolution are challenged accordingly.

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