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ARTICLES

Human Adaptation to the Control of Fire

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Charles Darwin attributed human evolutionary success to three traits. Our social habits and anatomy were important, he said, but the critical feature was our intelligence, because it led to so much else, including such traits as language, weapons, tools, boats, and the control of fire. Among these, he opined, the control of fire was "probably the greatest ever [discovery] made by man, excepting language."[1:48] Despite this early suggestion that the control of fire was even more important than tool use for human success, recent anthropologists have made only sporadic efforts to assess its evolutionary significance.[2,3] Here we use recent developments in understanding the role of cooked food in human diets to support the spirit of Darwin's offhand remark. We first consider the role of fire in increasing the net caloric value of cooked foods compared to raw foods, and hence in accounting for the unique pattern of human digestion. We then review the compelling evidence that humans are biologically adapted to diets that include cooked food, and that humans have a long evolutionary history of an obligate dependence on fire. Accordingly, we end by considering the influence of fire on various aspects of human biology. We pay particular attention to life history, and also briefly discuss effects on anatomy, behavior, and cognition.

Foraging serves multiple purposes, including obtaining amino acids, vitamins, and minerals, but energy gain is consistently found to be the most important criterion for animal foraging decisions because maximization of energy gain tends to have direct consequences for fitness.[4] This assumption has been validated by numerous studies of primates showing that even small increases in net energy gain lead to increases in female reproductive rate and/or offspring survival, such as in humans,[5] chimpanzees,[6] and baboons.[7]

An obvious implication from optimal foraging theory is that, like diet choice, patch choice, and foraging time, methods of processing food should be designed to maximize energy gain. Among humans, the predominant form of food processing is cooking, which has long been known to be a cultural universal that demands time, energy, and care (Fig. 1). Yet when Lévi-Strauss[8] hypothesized that cooking has no significant biological effects, no one objected to his idea. Only in the last decade has abundant evidence emerged that cooking consistently increases the energy obtainable from most foods.

Two kinds of evidence are particularly informative, though research on both is still at an early stage. First, body weight data show that humans who eat cooked diets have a more positive energy balance than do those who eat raw diets.[9] In the most extensive study, a cross-sectional survey of 513 long-term raw-foodists living in Germany, Koebnick and colleagues[10] found that body mass index was inversely correlated with both the proportion of raw food in the diet and the length of time since adoption of raw-foodism. All studies of human raw-foodists, as well as many comparisons of domestic or wild animals that eat cooked versus raw diets, lead to the same conclusion: The more cooked food in the diet, the greater the net energy gain.[9,11]

By studying the effects of cooking on specific nutrients, *in vivo* experiments have begun to reveal the mechanisms underlying the beneficial effects of cooking on energy availability. Until recently, researchers generally assumed that raw nutrients such as starch and protein are well digested by humans, given that when humans eat these nutrients raw, very little to none of the nutrient reaches the feces in an undigested form. The inference of 100% digestibility was flawed, however, because studies of ileostomy patients show that both raw starch and raw protein are only partially digested by the time they reach the end of the human small intestine. After leaving the ileum and entering the large intestine, residual nutrients are not digested by the gut. Instead, they are fermented by intestinal microbes, which consume a proportion of the resulting energy. The proportion of energy used by the microflora is unavailable to humans; that fraction

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Figure 1. Baboon being prepared for cooking in a Hadza camp, northern Tanzania. Following a widespread practice, the hunters have laid the prey on the fire in order to remove the hair by singeing. After the hair has gone, they sometimes leave the carcass on the fire and let it roast *in situ*. Alternatively, they boil the meat in a pot. Photograph and information courtesy of Frank W. Marlowe. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

of loss to humans ranges from 100% for protein[12,13] to an estimated 50% for carbohydrates.[14,15] Accordingly, based on the proportion of nutrient digested by the time it reaches the large intestine, cooking appears to increase digestibility substantially. Current experiments suggest that the associated caloric gain due to improved digestibility as a result of cooking is 12%–35% for starches (median = 30%: oats, wheat, plantain, potato and green banana), and 45%–78% for protein (chicken egg).[11] The energetic costs of cooking food are currently unmeasured, but would have to be very high to negate these benefits. For individuals able to obtain their food cooked without excessive difficulty in finding fuel and defending their fireplaces, these effects imply a large fitness advantage.

Cooking also increases net energy gain by reducing the metabolic work done by humans when digesting. Evidence for this claim comes from animal studies. Other things being equal, rats eating softer food expend less energy in digestion, and are therefore heavier and more obese than rats eating harder diets having the same number of measured calories.[16] Cooking consistently softens plant food,[9] and gelatinizes collagen and therefore reduces the physical integrity of meat,[17] so that similar effects can be expected as consequences of cooking. Although this hypothesis has not been directly tested in mammals, pythons fed cooked meat have been found to experience 12%–13% lower costs of digestion than do pythons fed equivalent meals of raw meat.[18]

Various other mechanisms are potentially important but have been less well studied.[11] Cooked lipids are likely to be digested more easily than are raw lipids because they tend to offer a greater surface area for digestion. Cooking may offer important benefits by reducing the energetic costs of detoxification or immune defense against pathogens. Cooking also allows more dry weight to be ingested because it reduces water content.

Given these energetic benefits of cooking, in addition to other advantages such as making food safer, more accessible, and more appetizing, why do people worldwide ever eat any of their diet raw? Two reasons appear to be particularly important. First, many fruits are designed to be eaten raw. That is, they are biologically and, in some cases, agriculturally adapted to be as attractive as possible to consumers because, as in the case of wild fruits, consumers disseminate swallowed or expectorated seeds. The principal attractant is most often sugar, as in apples and grapes. Cooking presumably does little to increase the digestibility of such items.

Second, cooking is sometimes impractical, particularly when individuals are on trek or foraging. For example, Australian aborigines would eat a variety of roots, eggs, or animals (such as mangrove worms) raw during the day, but if they found enough of the same items to bring back to camp, they would cook them after reaching home. Likewise Inuit hunters would rarely attempt to cook while foraging, since wood fuel was in short supply and most cooking relied on seal-oil burners that required several hours of use. Inuit men therefore ate various raw animal foods by day, including cached fish and caribou. On their return to camp, however, a cooked evening meal was the norm.[9]

BIOLOGICAL ADAPTATION TO COOKED FOOD

While most animals, whether wild or domestic, appear to resemble humans by gaining more energy from cooked food than from raw food, current evidence points to a remarkable difference between humans and all other species in the ability to thrive on raw food. Every animal species investigated to date fares acceptably on raw diets. Only humans do not. Thus, no cases are known to us of humans living on raw wild food for more than a few weeks. Raw domesticated food can provide a sustaining diet for contemporary urban raw-foodists, but the few studies of health status all indicate that urban raw-foodists are at risk of chronic energy shortage.

Inadequate energy gain from a raw diet probably explains a particularly telling result. Koebnick and colleagues[10] found that most women on a 100% raw diet were sub-fecund: approximately 50% of their subjects were amenorrheic. Indeed, like energy deficiency, the incidence of amenorrhea varied positively with the percentage of raw food in the diet and the duration of raw-foodism (Fig. 2). The odds of energy defi-

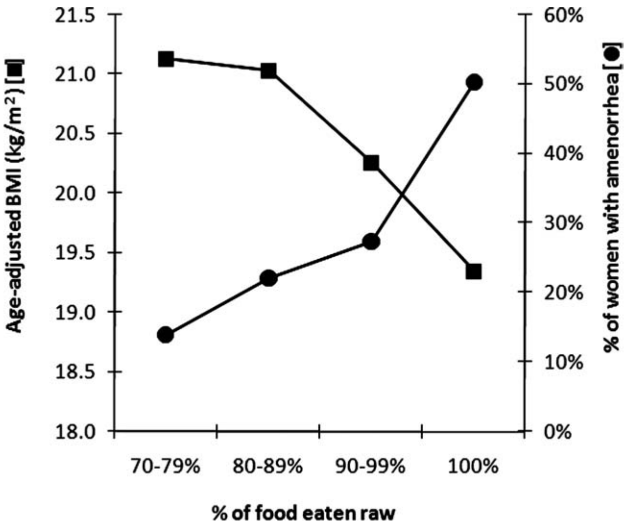

Figure 2. Energy deficiency among raw-foodists, adapted from Koebnick and colleagues.[10] Age-adjusted body mass index (left axis, ■) and percentage of nonpregnant female subjects <45 years old reporting amenorrhea (right axis, ●) as a function of the percent of the diet that is eaten raw. The odds of energy deficiency or amenorrhea were not different for vegans, vegetarians, or meat-eaters in this sample.

ciency or amenorrhea were not reduced in subjects who ate animal foods, suggesting that these results were driven by the lack of cooking rather than diet composition. It is notable that reproductive failure occurred in these women even though their urban raw diets had critical energetic advantages over raw diets that they hypothetically might have attempted to consume in the wild. First, since the urban foods were primarily domesticates (both plant and animal), they were likely high in digestible nutrients and low in indigestible components or toxins compared to wild raw foods. Second, the urban raw-foodists would have suffered little seasonal variation in food quality since they obtained food from global sources. Third, raw diets were extensively processed nonthermally (for example, in blenders) or even by drying over low heat. Many raw-foodists treat foods that have been heated below ~46°C as acceptable items. An additional advantage appears to come from the urban raw-foodists taking less exercise than foragers do.

The evidence that the average woman eating a diet of 100% raw high-quality foods is amenorrheic suggests an important conclusion: Human populations are not adapted to survive on a diet of raw wild food, even when it is extensively processed using nonthermal methods. This is consistent with the fact that no human population has ever been found living on raw wild food. The only alternative possibility is that hunter-gatherers in the unknown past were consistently able to find wild raw foods of higher quality than those eaten by contemporary urban raw-foodists. The challenge for those who are skeptical about the importance of cooking in human evolution is therefore to identify such diets. Even though honey, marrow, liver, and some exceptional other kinds of meat, fruit, or social insect might, in theory, sustain a population when eaten raw for a few weeks or months, we know of no raw diet that could provide predictable year-round adequacy. Until such a diet has been identified, we conclude that humans differ from all other species in being biologically committed to a diet of cooked food.

This proposal is easily understood in terms of our current biology. Most importantly, the few available measurements indicate that the intestines of humans are small compared to those of other primates, being about 60% of the expected weight/volume for a species of our body mass.[19] More data are needed to assess the variation in gut dimensions within species, but current information suggests that once our ancestors had predictable access to cooked food, there would have been little benefit in retaining a relatively capacious colon designed to allow fermentation of long-chain carbohydrates. Since gut tissue is energetically expensive to maintain, selection would have favored reduction of colonic tissue and other parts of the gut that were no longer useful for individuals eating a cooked diet.

Human molars are also smaller than those of other primates.[9] The action of cooking in reducing food toughness suggests that tooth size reduction is adaptive.[20] Other features of the mouth that have been interpreted as evolutionary responses to cooked foods include reduction of jaw-muscle myosin, increased salivary amylase production, and reduced oral cavity volume.[21]

Many other adaptations to cooked diets can be expected. Very little is known about the comparative enzymology of the human and ape digestive systems, but the relatively high quality of cooked food suggests that human-specific adaptations are likely. Reductions in toxin intake due to the destructive effect of heat may have led to increased sensitivity to plant xenobiotics in humans compared to many primates. Increased ingestion of Maillard compounds (potentially toxic complexes of sugars and amino acids that form under heat catalysis) could have selective consequences for detoxification systems. The ingestion of relatively high calorie loads in meals, particularly late in the day, suggests modifications to the insulin system in humans as compared to apes. Such possibilities make the evidence that humans are uniquely adapted to a high-quality diet of cooked food a provocative claim for understanding various aspects of human digestive physiology in a new way.

WHY *HOMO ERECTUS* APPEARS TO HAVE NEEDED FIRE

Given evidence that all humans are biologically adapted to a cooked diet, when did fire use begin? The archeological evidence gives us a minimum age of at least 250 kya. Several sites dated to 250 kya or older contain evidence of fire use by hominins, including burned deposits, fire-cracked rocks, reddened areas, baked clay, ash, charcoal, fire-hardened wood, burned lithics and bone, and even some indication of hearths.[22] Older dates for fire use are also widely acknowledged at sites such as Beeches Pit in England[23] and Schöningen in Germany,[24] dated to ∼400 kya, as well as Gesher Benot Ya'aqov in Israel, dated to 790 kya.[25] Unfortunately, the archeological record may never tell us when fire was first controlled. There is a decreasing probability of finding evidence of any type as time increases, and this is particularly true with fire use, since traces of fire can vanish quickly.[9] For example, Sergant, Crombé, and Perdaen[26] have reported that burned bone, shells, and other artifacts have been found at almost all Mesolithic sites in the northwest European Plain, yet direct evidence of control of fire is extremely limited.[26]

Biology provides an alternative method of inferring the origin of cooking. Animals show that anatomy can adapt very quickly to a change in diet.[27–29] Fast adaptation rates are also known for hominins. Among human populations with a history of dairying, lactase persistence (that is, the ability to digest lactose into adulthood) has evolved at least twice in the last 7,000 years.[30,31] In addition, populations with a recent history of consuming starch-rich foods exhibit higher copy numbers of the gene encoding for salivary amylase.[32] Consequently, we can reasonably infer the origin of cooking from the emergence in hominins of biological traits that are consistent with the consumption of cooked food.

The predictable effects of cooking, as noted earlier, include food softening (including enhanced fracturability) as well as increased digestibility and reduced costs of digestion. From these we can hypothesize that the adoption of cooking should have led to corresponding reductions in masticatory and gastrointestinal anatomy. In what hominin, if any, did such reductions take place?

We can eliminate *Homo sapiens* as a candidate, since fire was almost certainly controlled prior to their emergence ∼300–200 kya. Also, the anatomical differences between *H. heidelbergensis* and *H. sapiens* were not obviously diet-related, involving primarily a smaller face, a rounder head, and a somewhat larger brain.[33]

Homo heidelbergensis appears to be a reasonable candidate from an archeological perspective, since its emergence ∼800–600 kya corresponds to the earliest widely accepted date for the control of fire.[25] *H. heidelbergensis* differs from its precedessor, *H. erectus*, primarily by its larger cranial capacity and other aspects of cranial shape, including a higher forehead and a flatter face.[9] These features are not irrelevant: A less prognathic face can indicate reduced masticatory strain,[34] while a larger brain suggests a higher energy budget, since the brain is a metabolically expensive tissue.[19] It is therefore likely that some improvement in diet did occur at this junction. However, the anatomical changes appear too slight a response to a dietary shift as significant as cooking was likely to have been. In addition, the transition from *H. erectus* to *H. heidelbergensis* appears to have involved no major changes in dentition or gastrointestinal anatomy, in contrast to what would be predicted if *H. heidelbergensis* had been the first species to consume a cooked diet.

In contrast, the transition from late australopithecines or early *Homo* (*Homo habilis*, *H. rudolfensis*) to *H. erectus* is associated with significant changes in diet-related features that are consistent with the predicted effects of a cooked diet. Postcanine tooth area is smaller in *H. erectus* than in any previous hominin on an absolute basis, and so small as to be equivalent to *H. sapiens* when adjusted for body size.[35] Correspondingly, *H. erectus* exhibits a relatively smaller mandible[36] and other aspects of facial shortening, which suggest reduced masticatory strain.[34] Together, these craniodental features indicate that *H. erectus* was consuming a softer diet. Gut size also appears to conform to the expected pattern. For instance, *H. erectus* appears to have had a barrel-shaped thoracic cage similar to that of later *Homo* and distinct from the funnel-shaped thoraces of previous hominins.[37] *H. erectus* is therefore reconstructed as having a smaller gut than its ancestors did.[19] Given consistent trade-offs in gut versus brain size among primates,[19] larger cranial capacity in *H. erectus* (849 cm^3) than in *H. habilis* (601 cm^3) or *H. rudolfensis* (736 cm^3)[35] is also consistent with a smaller gut. Despite these reductions in digestive anatomy, *H. erectus* shows signals of increased energy use, including larger body size,[38] adaptations for long-distance running,[39] and possibly reduced interbirth intervals.[40] The apparently softer, more digestible, and higher energy diet of *H. erectus* are all consistent with the expected effects of cooking.

Locomotor adaptations also point to the control of fire by *Homo erectus*. It is generally accepted that *H. erectus* was the first obligate biped, with multiple adaptations for terrestrial locomotion that came at the expense of arboreal capability.[39,41–44] Obligate terrestriality would have exposed *H. erectus*, with a reduced capacity to scramble up a tree, to a broader array of predators, including lions, leopards, hyenas and saber-toothed cats.[45] Whereas *H. erectus* might have defended themselves with weapons during the day, it is hard to imagine how they would have defended themselves at night without the protection of fire.[46] Indeed, primates almost never sleep terrestrially. The main exceptions to this rule are humans, who universally rely on fire for protection in natural habitats; some gorillas (especially adult males), which are probably less susceptible to predation than were *H. erectus* on account of their larger body size and predator-poor forest habitat; and some cliff-sleeping baboons.[47] We therefore suggest that the control of fire was a prerequisite for the transition to obligate terrestriality.

ADAPTIVE CONSEQUENCES OF THE CONTROL OF FIRE

Life History

Life history theory predicts causal relationships between age-specific extrinsic mortality rates and the pace of life history. For example, higher extrinsic mortality in adults due to increased rates of predation or disease results in a smaller proportion of the population surviving to older age. Increased extrinsic mortality in adults is therefore expected to weaken selection on genetic factors that delay senescence.[48,49] As a result, investments in growth and maintenance are less likely to pay off in terms of increased fecundity. For this reason, populations with high adult extrinsic mortality tend to evolve fast life history patterns that feature earlier and heavier overall investments in reproduction. Correlated life history traits include shorter gestation, smaller size at birth, earlier weaning, a reduced growth period, smaller adult body size, earlier sexual maturity, shorter interbirth intervals, and a shorter life span. In contrast, species with low adult extrinsic mortality can afford to allocate more energy to growth and maintenance, favoring a life history pattern that features slow maturation, increased adult body size, late reproduction, high investment in each of a relatively small number of offspring, and longer life. These relationships have been extensively supported both in the wild[50–52] and experimentally.[53–55]

Compared to other mammals, primates tend to fall along the slow end of the life history continuum, even controlling for body size.[56] Humans, however, are unique among primates in having a mixed-pace life history (Fig. 3). In some respects, humans epitomize the slow strategy. For example, compared to chimpanzees, humans have larger infants, protracted juvenility (childhood), and longer adult life expectancy. Yet humans also wean early and reproduce at a much faster rate than would be expected by the pace of our life history. As Dean and Smith[57:115] have described it, reproduction in humans (hunter-gatherers) “works in double time compared to our closest relatives, the great apes,” with mean interbirth intervals in human foragers being just 2–4 years compared to 5–6 years in chimpanzees.[58,59]

Two main hypotheses have been proposed to explain the unusual combination of slow and fast features in human life history. Both note that humans are evolutionarily committed to a high-quality diet that is difficult to procure. They therefore conclude that weaned juveniles cannot easily feed themselves. As a result, juveniles need to be provisioned by mothers or other kin.[58]

The first hypothesis, proposed by Hawkes and colleagues,[60] emphasizes the role of skilled postreproductive women in provisioning juveniles and helping with child care. According to their idea, known as the “grandmother hypothesis,” women can add to their inclusive fitness after menopause by facilitating reproductive success in their daughters and other younger kin. In this scenario, longer-lived women contribute more to the gene pool via indirect fitness, leading natural selection to favor increased longevity. Interbirth intervals are reduced because the procurement, preparation, and provision of appropriate foods by grandmothers means that dependent offspring are weaned sooner, while mothers are better at and spend less energy in foraging, thus facilitating the resumption of menstrual cycling. Hawkes and colleagues[60] suggest that the high fitness benefits of being a grandmother may explain the evolution of postmenopausal longevity in humans. Thus, with respect to the life history paradox, the grandmother hypothesis suggests that, thanks to certain unique human traits, a long life promotes fast reproduction and vice versa.

The second hypothesis, which was proposed by Kaplan and colleagues,[58] emphasizes the age-specific pattern of productivity. According to their idea (the “embodied capital model”), productivity of food in adulthood is so high that it can predictably compensate for the negative productivity in early life through the intergenerational transfer of resources. Under this model, longevity is extended because the return from delayed investments increases as the productive life span increases. Interbirth intervals decrease through the system of intergenerational transfers (from any kin, not just grandmothers) that allow women to weight energy allocation toward reproduction rather than food production during their fecund years. Similar logic has been employed to argue for the inclusive fitness contributions of children and adolescents in shaping the unexpectedly “fast” component of the human life history pattern.[61,62]

Here we complement these ideas by proposing that the control of fire and consumption of cooked food also contributed to the evolution of the paradoxical human life history pattern. In our “control-of-fire hypothesis” the slow components of human life history were favored by two main consequences of using fire. First, fire use led to reduced extrinsic mortality as a result of lower predation and disease. Second, cooking raised the nutritional value of provisioned food, increasing the value of assistance from older individuals and thereby strengthening the selection pressures on senescence. The fast components of human life history, early weaning and short interbirth intervals, were likewise supported by cooking. In our model, earlier weaning was made possible by cooked foods being softer, more easily digestible, and less pathogen-bearing than raw foods. Reduced interbirth intervals were favored by both the energetic advantages of a cooked diet and the provisioning that cooking facilitates, allowing for greater stability in the nutritional status of mothers. These ideas are elaborated briefly below. Box 1 summarizes the commonalities and distinctions among the grandmother hypothesis,[60] embodied capital model,[58] and control-of-fire hypothesis.

Slow Life History via Reduced Extrinsic Mortality and Increased Productivity in the Elderly

The human transition to obligate terrestriality, apparently beginning with *Homo erectus*, should theoretically increase extrinsic mortality due to higher rates of predation, disease, and environmental hazards on the ground. As expected, a phylogenetically controlled analysis of 776 mammalian species has found that terrestrial taxa tend to have shorter maximum longevity

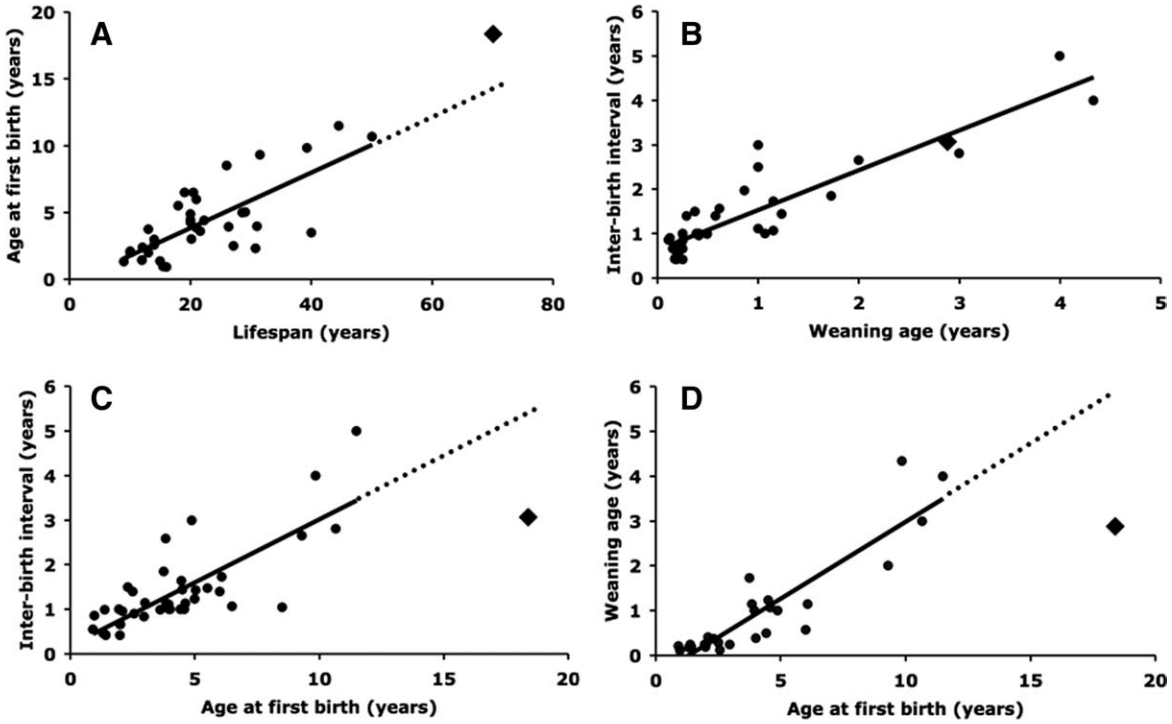

Figure 3. The human life history puzzle. In most species, different life history parameters are consistent in their pace, as illustrated here for nonhuman primate species (solid circles) by correlations among four life history variables. Unusually, hunter-gatherers (large diamond) are slow in two variables (life span, age at first birth), but fast in two others (weaning, interbirth interval). A: Nonhuman primates with long maximum life span tend to have late age of first birth ($r^2 = 0.56$, $n = 36$, $p < 0.001$). Humans are here assigned a conservative estimate of 70 years for maximum life span, following Harvey, Martin, and Clutton-Brock,[92] and fall close to the primate line. B: Nonhuman primates with later weaning have longer interbirth intervals ($r^2 = 0.80$, $n = 36$, $p < 0.001$). Hunter-gatherers conform to the primate trend. C: Nonhuman primates with a late age of first birth tend to have long interbirth intervals ($r^2 = 0.61$, $n = 41$, $p < 0.001$); however, hunter-gatherers have shorter interbirth intervals than expected. D: Nonhuman primates with a late age of first birth tend to wean later ($r^2 = 0.82$, $n = 29$, $p < 0.001$), but hunter-gatherers have an earlier weaning age than expected. The puzzle about humans is why they combine fast reproduction (short interbirth interval and early weaning) with slow growth (late age at first birth). Data sources: nonhuman primates, Harvey, Martin, and Clutton-Brock[92]; hunter-gatherers, Marlowe[89] (Table 2, warm-climate, nonequestrian only). Number of hunter-gatherer societies contributing to mean values: age at first birth, 6; interbirth interval, 9; weaning age, 18.

than do arboreal taxa.[63] Yet despite our terrestriality, modern humans were found to exhibit the highest longevity per body size of any mammal in the dataset, arboreal or terrestrial (Fig. 4). This is especially remarkable given that all other terrestrial primates reduce nocturnal predation by sleeping in trees or on cliffs. Aiello and Key[40:562] proposed that the solution to the problem of extended human longevity "most probably lies in the developing social organization and expanding brain that provided a cultural buffer to the elevated mortality risks of the savanna." We suggest that a particularly important "cultural buffer" was fire use.

The control of fire would have reduced extrinsic mortality by at least two means. First, the presence of fire appears to be a powerful deterrent of predators. Although no studies have formally quantified the deterrent effect of fire, demographic data support this claim. For example, the causes of 4,993 deaths in a population of 8,008 !Kung hunter-gatherers of the Nyae Nyae area, from ca. 1900 to 2005, were systematically collected by John Marshall, Claire Ritchie, and Polly Wiessner, and compiled into a database by Wiessner. Because predator attacks become legendary, Wiessner (personal communication) suspects that few, if any, are missing from the record. Wiessner's database includes 10 deaths or serious maulings by lion or leopard from 1910 to 1960, all but one of which occurred in the absence of fire. As these data imply, Wiessner reports that the !Kung regard a night-time fire as importantly protective. Thus, even though getting firewood can be a laborious task, the !Kung normally keep fires going all night and stoke them well when predators are in the vicinity, solely for protection. The danger of sleeping without a fire is illustrated by some of the fatal attacks, such as the death of /Asa: "Her mother and father were sleeping and had let the fire go dead. /Asa was sleeping a short distance away from them. The story goes that lions came and sat by the family, watched the parents, saw /Asa and took her" (P. Wiessner, personal communication).

Second, control of fire should reduce extrinsic mortality by lowering rates of disease. Controlled burning of campsites controls pest infestations.[64] In addition, cooking significantly reduces the incidence of foodborne illness, particularly for diets that include meat.[11] Heat kills the most common foodborne bacteria, including *Escherichia coli*, *Salmo-*

Box 1. Summaries of Three Solutions to the Human Life History Paradox: The "grandmother hypothesis,"[60] the "embodied capital model,"[58] and the "control-of-fire hypothesis."

A. Common framework. The three solutions are not mutually exclusive. All three models share a framework in which reduced extrinsic mortality (1) is responsible for "slow" aspects of human life history, notably slow maturation (2) and high longevity (3). An inverse relationship between extrinsic mortality (M) and time to maturity (α) is expected under Charnov's dimensionless approach to life history, in which αM is approximately constant across related taxa.[93] Slow maturation, in turn, promotes increased adult body mass.[a] Reduced extrinsic mortality will also favor increased longevity, as the average adult life span is roughly 1/M.[94] All three models also share the concept that the intensive provisioning of younger kin (4) allows for "fast" aspects of human life history, including earlier weaning of infants (5) and an earlier return to fecundity by women after weaning, which in turn favors a short interbirth interval (6) and high fertility overall. Whether stated or implied, all three models also infer that high fertility contributes to high longevity, since the inclusive fitness benefits that result from provisioning by older kin will act to strengthen natural selection on factors delaying senescence.

B. Grandmother hypothesis.[60] This model focuses on the inclusive fitness contributions of senior women as the critical factor allowing for high longevity and high fertility in humans. Extractive foraging by skilled postreproductive women generates food in excess of self-maintenance requirements (1) and this surplus is shared with juvenile relatives. This surplus food, as well as other contributions by post-reproductive women in the form of food processing and child care, allows for higher fertility of reproductive-aged kin. Since inclusive fitness rises for postreproductive women who provision, "long-lived helper" genes increase in frequency in the gene pool, contributing to longevity. In addition, continued provisioning by postreproductive women lowers the susceptibility to disease (2) of juvenile kin, further selecting for increased longevity. Hawkes and colleagues[60] argued that these relationships may explain the evolution of postmenopausal longevity in humans. The complementarity between the grandmother hypothesis and the control-of-fire hypothesis is illustrated by the fact that O'Connell, Hawkes, and Blurton Jones[77] discussed the importance of cooking as a mechanism that helped enable provisioning of kin.

C. Embodied capital model.[58] This model emphasizes the time required to learn to subsist effectively on a diet of high-quality, nutrient-dense foods. Here, slow maturation allows for the acquisition of knowledge, skill, and strength (1) which lead to profitable hunting and extractive foraging (2). The productivity of older individuals far exceeds that of younger individuals, leading to a system of resource transfers from old to young within kin groups. In addition, since hunting is a low-success but high-return activity, a dietary niche that involves hunting favors a broader culture of food sharing (3) (kin-based and nonkin-based). Jointly, kin provisioning and food sharing act to minimize volatility in nutritional status, resulting in less disease (4). In addition, such food transfers lead to less predation (5), since provisioning reduces the amount of time that juveniles must spend out of camp and since food sharing reduces the costs of group living, leading to larger group size. Increased knowledge, skill, and strength can further limit predation as they allow better defense. The resulting reduction in extrinsic mortality selects for the "slow" aspects of human life history, with high longevity subject to especially strong selection because cumulative resource production increases nonlinearly with longevity. Kaplan and colleagues[58] argued that these relationships lead to co-evolution between the human patterns of life history and extreme intelligence.

D. Control-of-fire hypothesis. We propose that the control of fire increases the efficiency of provisioning and reduces extrinsic mortality, thus contributing to the evolution of the human life history pattern.

Increased efficiency of provisioning: Fire use (1) allows for the cooking of food (2), which reliably enhances food energy, digestibility, and softness (3) by the mechanisms discussed in this paper. Suitable infant foods are generated, allowing earlier weaning. In addition, the high nutritive value of cooked food likely contributes to a short interbirth interval, given data illustrating the suppressive effect of a raw diet on ovarian function in modern raw-foodists.[10] Importantly, the effects of cooking improve the efficiency of provisioning, with fewer raw resources required to achieve the same benefit. This enhances the value of kin provisioning, thus broadening the number of potential provisioners. Moreover, the act of cooking represents a means of contribution. This may enable juveniles who are not yet efficient hunters or foragers to contribute meaningfully to kin provisioning and thereby gain inclusive fitness benefits. Jointly, these characteristics favor the "fast" aspects of human life history.

Reduced extrinsic mortality: Other effects of cooking include food detoxification and the killing of foodborne pathogens. These features, coupled with stable nutritional status as a result of a high-quality cooked diet and a culture of provisioning,

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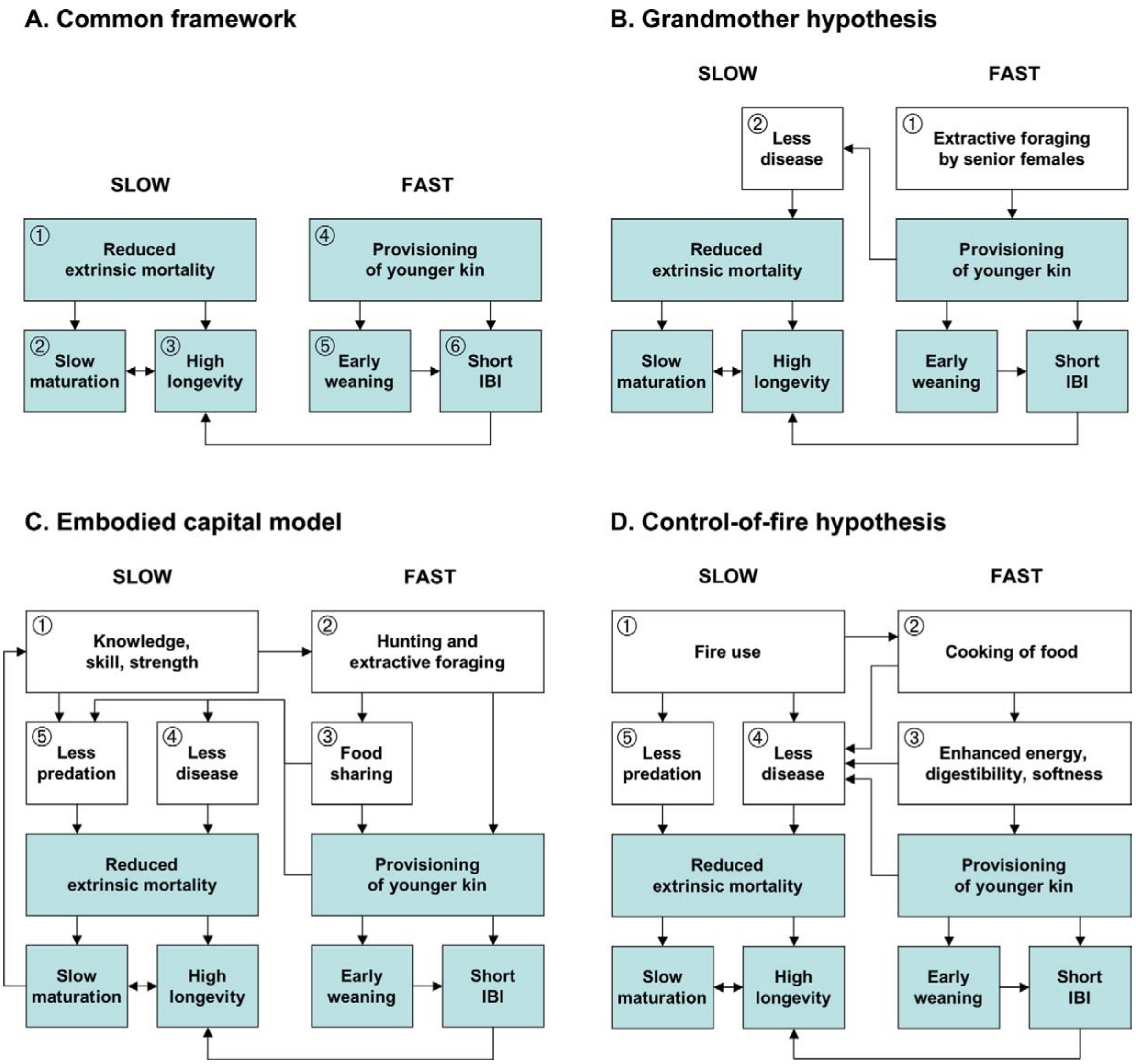
[a] Body mass increase in *Homo* is complicated by a reduction in sexual dimorphism, so that only females experience the increased mass. Reduction in sexual dimorphism in *Homo* is thought to be due to sexual selection,[95] which we do not discuss in the present paper.



lead to lower rates of disease (4). Disease risk may be lessened further by fire use, independently of the effects of cooking, if campsites are burned to eradicate pests. As discussed in this paper, fire use results in less predation (5) due to the effects of fire as a predator deterrent and potential weapon. Jointly, the suppressive effects of fire use on extrinsic mortality contribute to the “slow” aspects of human life history.

nella, *Campylobacter*, *Staphylococcus*, *Listeria*, and *Clostridium botulinum*, all of which are potentially lethal. In urban societies, the incidence of foodborne illness arising from meat consumption was recently estimated to be 99.98% lower due to cooking than it would have been if the same meats were consumed raw, suggesting that meat consumption at current levels would be energetically infeasible without cooking.[11] Finally, the fact that heat dramatically improves the energetic value of widely available food resources, such as tubers, reduces fluctuations in energy balance that might otherwise compromise immune functions.[65]

Importantly, beyond extrinsic factors, fire use can influence the selection pressures governing senescence. Two mechanisms have been proposed for senescence. The mutation accumulation theory, developed by Medawar,[48] states that the force of natural selection weakens with increasing age since extrinsic mortality will lead to fewer individuals alive in older age groups, even in a theoretically immortal population. Williams observed that antagonistic pleiotropy can also contribute to this effect, since traits that increase fitness early in life but bear a cost later in life will be positively selected for, given that more individuals are alive at young ages than at old ages.[49] According to these theories, any feature that increases the proportion of individuals surviving to later ages and allows aged individuals to increase their contributions to fitness will strengthen selection on genetic factors that delay senescence, leading to a slowing of life history. We suggest that cooking meets both criteria.

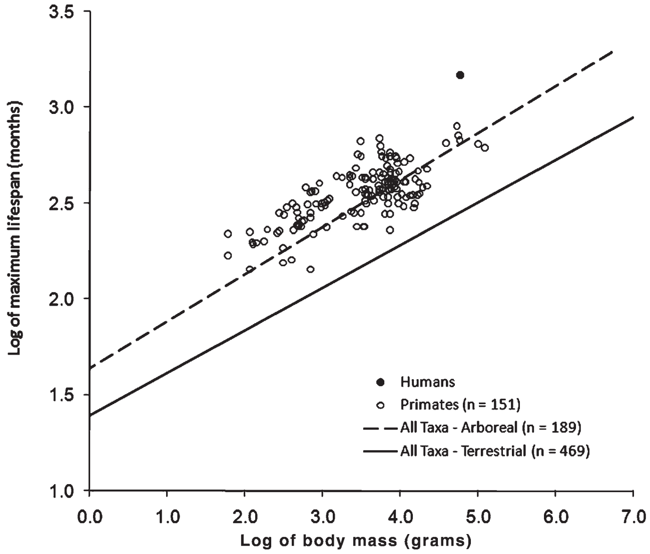


Figure 4. Maximal life span plotted against body mass for humans (closed circle) and 151 primates (open circles), compared to the ordinary least squares regressions for 189 arboreal mammals (dashed line: $0.25x + 1.64$, $r^2 = 0.50$, $p < 0.001$) and 469 terrestrial mammals ($y = 0.22x + 1.39$, $r^2 = 0.76$, $P < 0.001$). Modified from Figure 2 in Shattuck and Williams.[63]

For example, it is well established that edentulous or denture-wearing individuals have lower masticatory efficiency than do fully dentate individuals.[66] In addition, masticatory efficiency can be affected by age-related decreases in biting and chewing force,[67] which are attributable to deterioration in muscle strength.[68] Masticatory disability of this type has been shown to increase mortality, even after controlling for other risk factors.[69,70] By softening foods and reducing their toughness, cooking should improve the ability of aged individuals to meet their energy needs and thereby increase the proportion of individuals surviving to later ages.

In addition, by improving the energetic value of food resources, cooking should increase the advantages of assistance given to reproductive women by grandmothers[60] and other aged kin.[58] This increased contribution should lead to slower life history. Under the mutation accumulation model, it would strengthen selection against late-acting deleterious mutations by increasing the contribution to descendant gene pools of longer-lived individuals through the increased reproductive success of their female kin. Under the antagonistic pleiotropy model, it would increase payoffs for late somatic performance and therefore perturb the equilibrium in favor of higher longevity.

High Fertility via Cooked Food Consumption

By transforming plant and animal source foods into nutrient-dense, soft, and digestible forms via the mechanisms discussed above, cooking helps make foods accessible to the immature dentition and gastrointestinal tracts of potential weanlings. Moreover, unlike all other forms of processing, cooking reliably kills foodborne bacteria. Studies in developing countries have found that weaning diets are often contaminated with fecal pathogens due to improper food preparation and contact with animal feces, with microbial counts further worsened by prolonged storage at high ambient temperatures,[71,72] The difficulty of locating fuel for proper cooking or reheating of food has been identified as a key problem hindering the prevention of related enteric infections that are a primary cause of malnutrition among weanlings.[73] By increasing the availability of suitably nutritious and safe foods, cooking should facilitate weaning, shortening the duration of lactational amenorrhea.

Beyond lactational amenorrhea, it is well established that the primary ecological mediators of fecundity in women are energetic: net energy balance (that is, energy stores), energetic expenditure, nutritional intake (current weight gain or loss) and the energetic costs of lactation are all important.[74] For example, studies of natural fertility populations have found interbirth intervals to be negatively correlated with maternal postpartum weight, controlling for the duration of lactation.[75,76] By improving the energetic value of foods, particularly that of starch-rich foods that are consistently available, cooking enables a woman to resume ovarian cycling sooner. Indeed, given the high rates of ovarian suppression observed among female raw-foodists of reproductive age,[10] we posit that a cooked diet is necessary for routine fertility in female hunter-gatherers.

Since cooking improves the nutritive value of foods, fewer raw resources are required to achieve the same benefit. Given the well-established impact of cooking on starchy plant foods, which are the resources routinely collected by women among tropical hunter-gatherers, cooking should substantially lower a woman's foraging effort and increase her own net productivity. Therefore, unlike other models, our scenario for the impact of fire on human life history does not necessarily depend on extra-maternal provisioning of raw food resources or processing effort. Nevertheless, our scenario is highly compatible with extra-maternal provisioning. As discussed by O'Connell, Hawkes, and Blurton Jones,[77] this is because the positive effects of cooking increase the efficiency of kin provisioning, thereby broadening the range of provisioners who would achieve commensurate inclusive fitness benefits for their effort. Moreover, the act of cooking itself represents a means of contribution. This may enable juveniles who are not yet efficient hunters or foragers to contribute meaningfully to kin provisioning and thereby gain inclusive fitness benefits, provided that the inclusive fitness returns justify the costs in terms of time and energy. Observations of cooking behavior in Hadza juveniles as young as five, though limited to the exploitation of fires kindled by elders,[77] support the idea that contributions are possible even at very early ages. Thus, according to our model, provisioning by grandmothers, grandfathers, and juvenile kin can all be expected to play a role in the evolution of the unique human life history pattern.

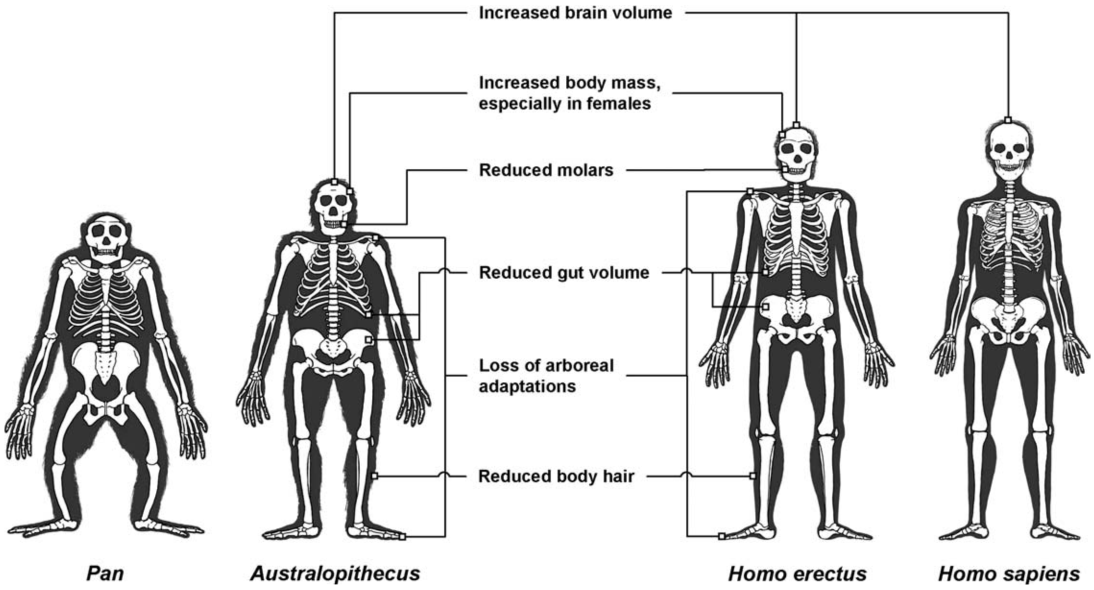
Anatomy

As with their effects on life history, cooking and other consequences of the control of fire appear to have influenced anatomy in multiple ways (Box 2). We have already suggested that cooking led to reduction of the digestive system in relation to body mass. Features of the human digestive system that have been reported to be relatively small include teeth, jaw musculature, oral cavity volume, total gut volume, and the surface areas of the stomach, large intestine (colon), and cecum.[9,78–80] The small intestine is the only major component of the human gut that is close to the expected size (smaller than in 62% of 42 measured primate species[78]), perhaps because it is the major site for nutrient absorption. No gut components are larger than expected. The diminution of the digestive system conforms to humans having a low daily dry weight intake of food compared to nonhuman primates.[81] On the other hand, total daily energy expenditure appears to be high for humans compared to other apes.[82] The contrast between reduced digestive structures and higher energy use is explicable only by human diets providing exceptional energy.

Aiello and Wheeler[19] proposed that gut reduction, and hence a reduction in the energetic cost of maintaining gut activity, contributes to solving the puzzle of large brains; that is, the problem of how humans satisfy the high energy demands of a big brain despite having the same relative basal metabolic rate as smaller-brained primates. Aiello and Wheeler considered that two dietary changes were responsible for the reduction of gut

Box 2. Fire and anatomical change.

Changes in anatomy putatively influenced by the control of fire. Although *Pan* and *Australopithecus* had important differences (such as walking quadrupedally and bipedally respectively) both are portrayed as having similar body mass, adaptations for climbing (e.g. robust, curved fingers and toes, narrow shoulders) and large guts, signaled by the flared shape of the rib-cage and wide pelvis. Based on such traits we assume that like *Pan*, *Australopithecus* slept at night in trees, climbed to eat fruits and some other arboreal items, and ate large volumes of food of relatively low caloric density compared to human diets. Critical changes resulting from the control of fire occur between *Australopithecus* and *Homo erectus*, with *H. erectus showing* the following features as described in the text. (1) Increased brain volume, supported by a reduction in gut volume made possible by the improved digestibility of cooked food. While there is evidence of increased brain volume in *Homo erectus*, the rise in cranial capacity was prominent throughout the Pleistocene and most noticeable in *Homo sapiens*. (2) Increased body mass, especially in females, promoted by reduced mortality due to fire use. (3) Reduced molar area, a result of food being softened by heat. (4) Reduced gut volume, indicated by a narrowing of the rib-cage and pelvis. (5) Loss of arboreal adaptations in the shoulders, arms, legs, hands and feet as arboreal foods grew less important than cooked terrestrial foods, and because *Homo erectus* could sleep on the ground following the control of fire. (6) Reduced body hair, with extra warmth achieved at night by resting near a campfire. (Anatomical drawings courtesy of Lucille Betti-Nash).



costs and corresponding increases in brain size: more meat around 1.9 mya, followed by cooking around 0.6 mya. In contrast, our argument that cooking likely arose with *Homo erectus* suggests that cooked food supported the rise in brain size from 1.9 mya onwards. As with many consequences of cooking, other factors may also play a role. In this case, reduction in skeletal muscle may also contribute to explaining how extra energy could be diverted to the brain.[83]

The problem of reducing heat loss when inactive suggests an effect of the control of fire on body hair. As Pagel and Bodmer[84] suggested, the ability to sleep next to a campfire would have solved the problem of maintaining warmth when asleep and therefore allowed the reduction of body hair. Loss of body hair could be favored by various factors, including reduced vulnerability to parasites[84] and increased ability to lose heat by day,[85] as well as at least nine other possibilities.[86] If Wheeler's heat-loss hypothesis is correct, the warmth provided by fire can therefore ultimately be considered vital in enabling humans to acquire the ability to run long distances. Anatomical evidence that long-distance running began with *Homo erectus*[39] is thus consistent with the idea that *H. erectus* controlled fire. Babies, being relatively inactive by day, would still need to be protected from hypothermia: this might explain why, unlike adults, they have a thick layer of heat-generating fat close to the skin.[87]

Behavior and Cognition

One of the most striking behavioral apomorphies of humans is that we spend much less time eating than nonhuman apes do. Great apes spend 4–7 hours per day chewing, much as expected from their large body mass. In contrast, humans spend less than one hour per day chewing, according to studies of U.S. residents, the Ye'kwana of Venezuela, Kipsigis of Kenya, South Pacific Samoans, and nine other societies.[9] In some ways, the abbreviated human chewing pattern makes us seem like a carnivore, since carnivores, as compared to plant eaters, spend a similarly small amount of time chewing their food.[88] However, carnivores achieve their low chewing time by rapidly slicing and swallowing large chunks of meat, which is unlike the human pattern of finely comminuting food. The short chewing time of humans is therefore better explained by the effect of cooking and nonthermal processing in reducing the toughness and hardness of food, than by the incorporation of increased amounts of meat in the diet.

Low chewing time in humans has several important consequences. Critically, individuals can afford to forego chewing for long periods during the day and instead compress much of their food intake into a relatively brief evening meal. As a result, instead of spending the majority of daylight hours with guts that are actively digesting, humans can minimize gut activity in favor of aerobic exercise. This allows relatively efficient multi-hour locomotion and long day journeys. Thus, male chimpanzees have average day ranges of 3–5 km, with an occasional maximum around 10 km, whereas male hunter-gatherers average around 9–14 km per day.[89] Such long day ranges appear to be facilitated by the combination of short chewing times and relatively quiescent guts.

In addition, the fact that humans can eat more than 2,000 calories in an hour of chewing means that they can cover their energetic needs even after returning to camp at the end of a largely unproductive day. This depends, of course, on food being available following their return. Among contemporary foragers, the household system means that married men can expect a cooked meal to be available every evening. This system, which allows men to forage for high-risk, high-gain food by supporting them nutritionally on days when they fail to produce, thus depends on the use of a food type that can be consumed rapidly; that is, cooked food. The tendency for men toforage more for high-risk, high-gain foods, while women specialize on low-risk, low-gain foods, must therefore have been strongly promoted by the control of fire.

The relationship between the control of fire and cognitive ability is speculative, but considerable mental ability clearly was important for launching the control of fire. The management of fire requires problem-solving (for example, to capture fire) and planning (for example, to get fuel). While chimpanzees and bonobos can control fire in limited ways,[9] it seems likely that hominin encephalization, possibly as a result of increased meat-eating by habilines, made the stable control of fire cognitively possible. After the control of fire was achieved, life history effects favoring a long period of childhood development would have created further opportunities for enhanced cognitive function. Various consequences would have followed. Even if the initial control of fire did not necessitate a stable home base for weeks at a time, central-place foraging was likely adopted to allow both fireside cooperation in cooking and food distribution, as well as caring for relatively immobile offspring. Reliance on fire also suggests a relatively high level of coordination compared to great apes. Given that great apes demonstrate a preference for cooked food,[90] we assume that the control of fire would have led rapidly to cooking, which then favored increased patience (to wait until the food is ready), cooperation, and respect for ownership in reducing the problem of scroungers taking food from a poorly guarded fire. Complex co-evolutionary pressures, including social pressures arising both from the opportunity to provision each other and from the ability to steal from each other, therefore seem likely to have shaped the relationship between fire and cognition.

CONCLUSION

We have presented evidence that the first species adapted to the control of fire was *Homo erectus*. We have also proposed various consequences of using fire, including contributions to the unique patterns of human life history. In some ways, we regard these ideas as conforming to existing theory. For instance, the hypothesis of early fire use does not challenge the idea that increased meat-eating played an important role in human origins. Nor do we conclude that the life style and life history of *H. erectus* were fully modern. The value of fire to humans and the nature of its use probably changed after fire was first controlled, thanks to advances both in cooking methods and other technologies, such as the effectiveness of fire-based defense against predators. The postulated effects of fire may therefore also have developed in stages. For example, while the initial control might have allowed hominids to sleep on the ground without experiencing an increase in predation rates compared to sleeping in trees, fire need not have had any immediate effects in lowering extrinsic mortality. The effects of controlling fire thus need to be considered without assuming that they were always the same as they are now.

Nevertheless, while the consequences of controlling fire have evolved, the acquisition of fire is clearly expected to have had large effects on numerous aspects of human biology, and in some ways our ideas confront conventional wisdom. For example, our hypothesis lies in contrast to the view that fire was controlled first by a relatively late member of the human lineage (that is, within the last half-million years), since that idea also necessitates the notion that fire use had little impact on human evolutionary biology. Likewise, it challenges the idea that humans are such ecological generalists that they are not adapted to any specific components of their habitats. Potts[91:129] exemplified a widely held view: "It is patently incorrect to characterize the human ancestral environment as a set of specific repetitive elements, statistical regularities, or uniform problems which the cognitive mechanisms unique to humans are designed to solve." In contrast, we claim that humans are biologically adapted to eating cooked food. Accordingly, the human ancestral environment required the presence of controlled fire and cooked meals, and thus presented humans with a specific and consistent set of problems relevant to their biology, behavior, and cognition.

The cooking hypothesis could be disproved by the discovery of some previously unknown combination of raw, nonthermally processed foods that provides an adequate human diet in diverse and variable habitats. Such a discovery would be provocative and informative. But if the cooking hypothesis is right, it presents numerous exciting challenges for understanding the evolutionary impact of the control of fire. Either way, further attention to the unique aspects of human dietary adaptation promises large rewards for understanding human evolution.

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