



# Human Adaptation to the Control of Fire

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Human adaptation to the control of fire

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

16

### 17 **The energetic consequences of cooking**

18 Foraging serves multiple purposes, including obtaining amino acids, vitamins and  
19 minerals, but energy gain is consistently found to be the most important criterion for animal  
20 foraging decisions because maximization of energy gain tends to have direct consequences for  
21 fitness.<sup>3,4</sup> This assumption has been validated by numerous studies of primates showing that even  
22 small increases in net energy gain lead to increases in female reproductive rate and/or offspring  
23 survival, e.g. in humans,<sup>5</sup> chimpanzees<sup>6</sup> and baboons.<sup>7</sup>

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

31 Two kinds of evidence are particularly informative, though research on both is still at an  
32 early stage. First, body weight data show that humans have a more positive energy balance when  
33 eating cooked diets compared to when eating raw diets.<sup>9</sup> In the most extensive study, a cross-  
34 sectional survey of 513 long-term raw-foodists living in Germany, Koebnick and colleagues  
35 found that body mass index was inversely correlated with both the proportion of raw food in the  
36 diet and the length of time since adoption of raw-foodism.<sup>10</sup> All studies of human raw-foodists,  
37 and many comparisons of domestic or wild animals on cooked versus raw diets, lead to the same  
38 conclusion: the more cooked food in the diet, the greater the net energy gain.<sup>9,11</sup>

39 Second, by studying the effects of cooking specific nutrients, experiments *in vivo* have  
40 begun to reveal the mechanisms underlying the beneficial effects of cooking on energy  
41 availability. Until recently researchers generally assumed that raw nutrients such as starch and  
42 protein are well digested by humans, given that when humans eat these nutrients raw, very little  
43 to none of the nutrient reaches the feces in an undigested form. The inference of 100%  
44 digestibility was flawed, however, because studies of ileostomy patients show that both raw  
45 starch and raw protein are only partially digested by the time they reach the end of the human  
46 small intestine. After leaving the ileum and entering the large intestine, residual nutrients are not

47 digested by the gut. Instead, they are fermented by intestinal microbes, which consume a  
48 proportion of the resulting energy. The proportion of energy that is used by the micro-flora is  
49 unavailable to humans, and the fraction of loss to humans ranges from 100% for protein<sup>12,13</sup> to an  
50 estimated 50% for carbohydrates.<sup>14,15</sup> Accordingly, based on the proportion of nutrient digested  
51 by the time it reaches the large intestine, cooking appears to increase digestibility substantially.  
52 Current experiments suggest that the associated caloric gain due to improved digestibility as a  
53 result of cooking is 12-35% for starches (median = 30%: oats, wheat, plantain, potato and green  
54 banana), and 45-78% for protein (chicken egg).<sup>11</sup> The energetic costs of cooking food are  
55 currently unmeasured but would have to be very high to negate these benefits. For individuals  
56 able to obtain their food cooked without excessive difficulty in finding fuel, defending their  
57 fireplace, etc., these effects imply a large fitness advantage.

58         Cooking also increases net energy gain by reducing the metabolic work performed by  
59 humans when digesting. Evidence for this claim comes from animal studies. Other things being  
60 equal, rats eating softer food expend less energy in digestion, and are therefore heavier and more  
61 obese than rats eating harder diets having the same number of measured calories.<sup>16</sup> Since  
62 cooking consistently softens plant food,<sup>9</sup> as well as gelatinizes collagen and therefore reduces the  
63 physical integrity of meat,<sup>17</sup> similar effects can be expected due to cooking. Although this  
64 hypothesis has not been tested directly in mammals, pythons fed cooked meat were found to  
65 experience costs of digestion that were 12-13% lower than pythons fed equivalent meals of raw  
66 meat.<sup>18</sup>

67         Various other mechanisms are potentially important but less well-studied.<sup>11</sup> Cooked  
68 lipids are likely to be digested more easily than raw lipids because they tend to offer a greater  
69 surface area for digestion. Cooking may offer important benefits by reducing the energetic costs

70 of detoxification or of immune defense against pathogens. Cooking also allows more dry weight  
71 to be ingested because it reduces water content.

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

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

87

### 88 **Biological adaptation to cooked food**

89         While most animals, whether wild or domestic, appear to resemble humans by gaining  
90 more energy from cooked food than from raw food, current evidence points to a remarkable  
91 difference between humans and all other species in the ability to thrive on raw food. Every  
92 animal species investigated to date fares acceptably on raw diets. Only humans do not. Thus no

93 cases are known to us of humans living on raw wild food for more than a few weeks. Raw  
94 domesticated food can provide a sustaining diet for contemporary urban raw-foodists, but the  
95 few studies of health status all indicate that urban raw-foodists are at risk of chronic energy  
96 shortage.

97         Inadequate energy gain from a raw diet probably explains a particularly telling result.  
98 Koebnick and colleagues found that most women on a 100% raw diet were sub-fecund:  
99 approximately 50% of their subjects were amenorrheic.<sup>10</sup> Indeed, like energy deficiency, the  
100 incidence of amenorrhea varied positively with the percentage of raw food in the diet and the  
101 duration of raw-foodism (Figure 2). The odds of energy deficiency or amenorrhea were not  
102 reduced in subjects who ate animal foods, suggesting that these results were driven by the lack of  
103 cooking rather than diet composition. It is notable that reproductive failure occurred in these  
104 women even though their urban raw diets had critical energetic advantages over raw diets that  
105 hypothetically they might have attempted to consume in the wild. First, since the urban foods  
106 were primarily domesticates (both plant and animal), they were likely high in digestible nutrients  
107 and low in indigestible components or toxins compared to wild raw foods. Second, the urban  
108 raw-foodists would have suffered little seasonal variation in food quality since they obtained  
109 food from global sources. Third, raw diets were extensively processed non-thermally (e.g. in  
110 blenders) or even by drying over low heat: many raw-foodists treat foods that have been heated  
111 below ~46°C as acceptable items. Finally, additional advantage appears to come from the urban  
112 raw-foodists taking less exercise than foragers.

113         The evidence that the average woman eating a diet of 100% raw high-quality foods is  
114 amenorrheic suggests an important conclusion: human populations are not adapted to survive on  
115 a diet of raw wild food, even when it is extensively processed using non-thermal methods. This



116 idea is consistent with the fact that no human population has ever been found living on raw wild  
117 food. The only alternative possibility is that hunter-gatherers in the unknown past were  
118 consistently able to find wild raw foods of higher quality than those eaten by contemporary  
119 urban raw-foodists. The challenge for those who are skeptical of the importance of cooking in  
120 human evolution is therefore to identify such diets. Even though honey, marrow, liver and some  
121 exceptional other kinds of meat or fruit or social insect might in theory sustain a population when  
122 eaten raw for a few weeks or months, we know of no raw diet that could provide predictable  
123 year-round adequacy. Until such a diet has been identified, we conclude that humans differ from  
124 all other species in being biologically committed to a diet of cooked food.

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

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

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

149

### 150 **Why *Homo erectus* appears to have needed fire**

151 Given evidence that all humans are biologically adapted to a cooked diet, when did fire  
152 use begin? The archeological evidence gives us a minimum age of at least 250 kya. Several sites  
153 dated to 250 kya or older contain evidence of fire use by hominids, including burned deposits,  
154 fire-cracked rocks, reddened areas, baked clay, ash, charcoal, fire-hardened wood, burned lithics  
155 and bone, and even some indication of hearths.<sup>22</sup> Older dates for fire use are also widely  
156 acknowledged at sites such as Beeches Pit in England<sup>23</sup> and Schöningen in Germany,<sup>24</sup> dated to  
157 ~400 kya, as well as Gesher Benot Ya'akov in Israel, dated to 790 kya.<sup>25</sup> Unfortunately, the  
158 archeological record may never tell us when fire was first controlled. There is a decreasing  
159 probability of finding evidence of any type as time increases, and this is particularly true with  
160 fire use, since traces of fire can vanish quickly.<sup>9</sup> For example, Sergeant and colleagues report that

161 burnt bone, shells and other artifacts have been found at almost all Mesolithic sites in the  
162 northwest European Plain, yet the direct evidence for control of fire is extremely limited.<sup>26</sup>

163 Biology provides an alternative method of inferring the origin of cooking. Animals show  
164 that anatomy can adapt very quickly to a change in diet,<sup>27,28,29</sup> Fast rates are also known for  
165 hominins. Among human populations with a history of dairying, lactase persistence (i.e. the  
166 ability to digest lactose into adulthood) has evolved at least twice in the last 7,000 years.<sup>30,31</sup> In  
167 addition, populations with a recent history of consuming starch-rich foods exhibit higher copy  
168 numbers of the gene encoding for salivary amylase.<sup>32</sup> Consequently, we can reasonably infer the  
169 origin of cooking from the emergence in hominins of biological traits that are consistent with the  
170 consumption of cooked food.

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

176 We can eliminate *Homo sapiens* as a candidate, since fire was almost certainly controlled  
177 prior to their emergence ~300-200 kya and since the anatomical differences from *H.*  
178 *heidelbergensis* were not obviously diet-related, involving primarily a smaller face, rounder head  
179 and a somewhat larger brain.<sup>33</sup>

180 *Homo heidelbergensis* would appear to be a reasonable candidate from an archeological  
181 perspective, since its emergence ~800-600 kya corresponds to the earliest widely accepted date  
182 for the control of fire.<sup>25</sup> *H. heidelbergensis* differs from its predecessor, *H. erectus*, primarily by  
183 its larger cranial capacity and other aspects of cranial shape, including a higher forehead and a

184 flatter face.<sup>9</sup> These features are not irrelevant: a less prognathic face can indicate reduced  
185 masticatory strain<sup>34</sup> and a larger brain suggests a higher energy budget, since the brain is a  
186 metabolically expensive tissue.<sup>19</sup> It is therefore likely that some improvement to the diet did  
187 occur at this junction. However, the anatomical changes appear too slight a response to a dietary  
188 shift as significant as cooking was likely to have been. In addition, the transition from *H. erectus*  
189 to *H. heidelbergensis* appears to have involved no major changes in dentition or gastrointestinal  
190 anatomy, in contrast to would be predicted if *H. heidelbergensis* were consuming a cooked diet.

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

206 apparently softer, more digestible, and higher energy diet of *H. erectus* are all consistent with the  
207 expected effects of cooking.

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

220

## 221 **Adaptive consequences of the control of fire**

### 222 **Life history**

223 Life history theory predicts causal relationships between age-specific extrinsic mortality  
224 rates and the pace of life history. For example, higher extrinsic mortality in adults – due to  
225 increased rates of predation or disease – results in a smaller proportion of the population  
226 surviving to older age. Increased extrinsic mortality in adults is therefore expected to weaken  
227 selection on genetic factors that delay senescence.<sup>48,49</sup> As a result investments in growth and  
228 maintenance are less likely to pay off in terms of increased fecundity. For this reason populations

229 with higher adult extrinsic mortality tend to evolve fast life history patterns that feature earlier  
230 and heavier overall investments in reproduction. Correlated life history traits include shorter  
231 gestation, smaller size at birth, earlier weaning, reduced growth period, smaller adult body size,  
232 earlier sexual maturity, shorter interbirth intervals, and shorter lifespan. By contrast, species with  
233 lower adult extrinsic mortality can afford to allocate more energy to growth and maintenance,  
234 selecting for a life history pattern that features slow maturation, increased adult body size, late  
235 reproduction, high investment in each of a relatively small number of offspring, and longer life.  
236 These relationships have been extensively supported both in the wild<sup>50-52</sup> and experimentally.<sup>53-55</sup>

237         Compared to other mammals, primates tend to fall along the slow end of the life history  
238 continuum, even controlling for body size.<sup>56</sup> Humans, however, are unique among primates in  
239 having a mixed-pace life history (Figure 3). In some respects, humans epitomize the slow  
240 strategy. For example, compared to chimpanzees, we birth larger infants, have protracted  
241 juvility (i.e. childhood) and longer adult life expectancy. Yet humans also wean early and  
242 reproduce at a much faster rate than would be expected by the pace of our life history. As Dean  
243 and Smith describe it, reproduction in humans (hunter-gatherers) “works in double time  
244 compared to our closest relatives, the great apes” (p. 115),<sup>57</sup> with mean interbirth intervals in  
245 human foragers being just 2-4 years compared to 5-6 in chimpanzees.<sup>58,59, 88</sup>

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

251           The first hypothesis was proposed by Hawkes and colleagues and emphasizes the role of  
252 skilled, post-reproductive women in provisioning juveniles and helping with childcare.<sup>60</sup>  
253 According to their idea, known as the “grandmother hypothesis,” women can add to their  
254 inclusive fitness after menopause by facilitating reproductive success in their daughters and other  
255 younger kin. In this scenario longer-lived women contribute more to the gene pool via indirect  
256 fitness, leading natural selection to favor increased longevity. Interbirth intervals are reduced  
257 because the procurement, preparation and provision of appropriate foods by grandmothers means  
258 that dependent offspring are weaned sooner; and mothers are better at (and spend less energy in)  
259 foraging, facilitating the resumption of menstrual cycling. Hawkes and colleagues suggest that  
260 the high fitness benefits of being a grandmother may explain the evolution of postmenopausal  
261 longevity in humans. Thus with respect to the life history paradox, the grandmother hypothesis  
262 suggests that thanks to certain unique human traits, a long life promotes fast reproduction, and  
263 vice versa.

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

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

288 *Slow life history via reduced extrinsic mortality and increased productivity in the elderly*

289 The human transition to obligate terrestriality, apparently beginning with *Homo erectus*,  
290 should theoretically increase extrinsic mortality due to higher rates of predation, disease and  
291 environmental hazards on the ground. As expected, a phylogenetically controlled analysis of 776  
292 mammalian species found that terrestrial taxa tended to have shorter maximum longevity than  
293 arboreal taxa.<sup>63</sup> Yet despite our terrestriality, modern humans were found to exhibit the highest  
294 longevity per body size of any mammal in the dataset, arboreal or terrestrial (Figure 4). This is  
295 especially remarkable given that all other terrestrial primates reduce nocturnal predation by  
296 sleeping in trees or on cliffs. Aiello and Key proposed that the solution to the problem of



297 extended human longevity “most probably lies in the developing social organization and  
298 expanding brain that provided a cultural buffer to the elevated mortality risks of the savanna” (p.  
299 562).<sup>40</sup> We suggest that a particularly important ‘cultural buffer’ was fire use.

300         The control of fire would have reduced extrinsic mortality by at least two means. First,  
301 the presence of fire appears to be a powerful deterrent of predators. Although no studies have  
302 formally quantified the deterrent effect of fire, demographic data support this claim. For  
303 example, causes of 4,993 deaths in a population of 8,008 !Kung hunter-gatherers of the Nyae  
304 Nyae area, from ca. 1900 to 2005, were collected systematically by John Marshall, Claire Ritchie  
305 and Polly Wiessner, and compiled into a database by Wiessner. Because predator attacks become  
306 legendary, Wiessner (pers. comm.) suspects that few, if any, are missing from the record.  
307 Wiessner's database includes 10 deaths or serious maulings by lion or leopard from 1910 to  
308 1960, all but one of which occurred in the absence of fire. As implied by these data, Wiessner  
309 reports that the !Kung regard a night-time fire as importantly protective. Thus, even though  
310 getting firewood can be a laborious task, the !Kung normally keep fires going all night and stoke  
311 them well when predators are in the vicinity, solely for protection. The danger of sleeping  
312 without a fire is illustrated by some of the fatal attacks, such as the death of /Asa: “Her mother  
313 and father were sleeping and had let the fire go dead. /Asa was sleeping a short distance away  
314 from them. The story goes that lions came and sat by the family, watched the parents, saw /Asa  
315 and took her” (P. Wiessner, pers. comm.).

316         Second, control of fire should reduce extrinsic mortality by lowering rates of disease.  
317 Controlled burning of campsites controls pest infestations.<sup>64</sup> In addition, cooking significantly  
318 reduces the incidence of foodborne illness, particularly for diets that include meat.<sup>11</sup> Heat kills  
319 the most common foodborne bacteria, including *Escherichia coli*, *Salmonella*, *Campylobacter*,

320 *Staphylococcus*, *Listeria*, and *Clostridium botulinum*, all of which are potentially lethal. The  
321 incidence of foodborne illness in urban societies arising from meat consumption was recently  
322 estimated to be 99.98% lower due to cooking than if the same meats were consumed raw,  
323 suggesting that meat consumption at current levels would be energetically infeasible without  
324 cooking.<sup>11</sup> Finally, the ability of heat to dramatically improve the energetic value of widely  
325 available food resources, such as tubers, reduces fluctuations in energy balance that might  
326 otherwise compromise immune functions.<sup>65</sup>

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

338         For example, it is well established that edentulous or denture-wearing individuals have  
339 lower masticatory efficiency than fully dentate individuals.<sup>66</sup> In addition, masticatory efficiency  
340 can be affected by age-related decreases in biting and chewing force,<sup>67</sup> attributable to  
341 deterioration in muscle strength.<sup>68</sup> Masticatory disability of this type has been shown to increase  
342 mortality, even after controlling for other risk factors.<sup>69,70</sup> By softening foods and reducing their

343 toughness, cooking should improve the ability of aged individuals to meet their energy needs and  
344 thereby increase the proportion of individuals surviving to later ages.

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

353         *High fertility via cooked food consumption*

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

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

375           Since cooking improves the nutritive value of foods, fewer raw resources are required to  
376 achieve the same benefit. Given the well-established impact of cooking on starchy plant foods,  
377 which are the resources routinely collected by women among tropical hunter-gatherers, cooking  
378 should substantially lower a woman's foraging effort and increase her own net productivity.  
379 Therefore, unlike other models, our scenario for the impact of fire on human life history does not  
380 necessarily depend on extra-maternal provisioning of raw food resources or processing effort.  
381 Nevertheless, our scenario is highly compatible with extra-maternal provisioning. As discussed  
382 by O'Connell and colleagues, this is because the positive effects of cooking increase the  
383 efficiency of kin provisioning, thereby broadening the range of provisioners that would achieve  
384 commensurate inclusive fitness benefits for their effort.<sup>77</sup> Moreover, the act of cooking itself  
385 represents a means of contribution. This may enable juveniles who are not yet efficient hunters  
386 or foragers to contribute meaningfully to kin provisioning and thereby gain inclusive fitness  
387 benefits, provided that the inclusive fitness returns justify the costs in terms of time and energy.

388 Observations of cooking behavior in Hadza juveniles as young as five, though limited to the  
389 exploitation of fires kindled by elders,<sup>77</sup> support the idea that contributions are possible even at  
390 very early ages. Thus, according to our model, provisioning by grandmothers, grandfathers and  
391 juvenile kin can all be expected to play a role in the evolution of the unique human life history  
392 pattern.

### 393 **Anatomy**

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

406 Aiello and Wheeler proposed that gut reduction, and hence a reduction in the energetic  
407 cost of maintaining gut activity, contributes to solving the puzzle of large brains, i.e. the problem  
408 of how humans satisfy the high energy demands of a big brain despite having the same relative  
409 basal metabolic rate as smaller-brained primates.<sup>19</sup> Aiello and Wheeler considered that two  
410 dietary changes were responsible for reduction of gut costs and corresponding increases in brain

411 size: more meat around 2 mya, followed by cooking around 0.6 mya. By contrast our argument  
412 that cooking likely arose with *Homo erectus* suggests that cooked food supported the rise in  
413 brain size from 1.9 mya onwards. As with many consequences of cooking, other factors may also  
414 play a role. In this case, reduction in skeletal muscle may also contribute to explaining how extra  
415 energy could be diverted to the brain.<sup>83</sup>

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

427

## 428         **Behavior and cognition**

429         One of the most striking behavioral apomorphies of humans is that we spend much less  
430 time eating than non-human apes do. Great apes spend 4-7 hours per day chewing, much as  
431 expected from their large body mass. By contrast humans spend less than one hour per day  
432 chewing according to studies of US residents, Ye'kwana of Venezuela, Kipsigis of Kenya, South  
433 Pacific Samoans and nine other societies.<sup>9</sup> In some ways the abbreviated human chewing pattern

434 makes us seem like a carnivore, since carnivores spend a similarly small amount of time chewing  
435 their food compared to plant-eaters.<sup>88</sup> However, carnivores achieve their low chewing time by  
436 rapidly slicing and swallowing large chunks of meat, unlike the human pattern of finely  
437 comminuting their food. The short chewing time of humans is therefore better explained by the  
438 effect of cooking and non-thermal processing in reducing the toughness and hardness of food,  
439 than by the incorporation of increased amounts of meat in the diet.

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

449         Additionally, the fact that humans can eat 2,000+ calories in an hour of chewing means  
450 that they can cover their energetic needs even after returning to camp at the end of a largely  
451 unproductive day. This depends, of course, on food being available following their return.  
452 Among contemporary foragers, the household system means that married men can expect a  
453 cooked meal to be available for them every evening. This system, which allows men to forage  
454 for high-risk, high-gain food by supporting them nutritionally on days when they fail to produce,  
455 thus depends on the use of a food-type that can be consumed rapidly, i.e. cooked food. The

456 tendency for men to forage more for high-risk, high-gain foods, while women specialize on low-  
457 risk, low-gain foods, therefore, must have been strongly promoted by the control of fire.

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

476

477         **Conclusion**



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

491           Nevertheless, while the consequences of controlling fire have themselves evolved, the  
492 acquisition of fire is clearly expected to have had large effects on numerous aspects of human  
493 biology, and in some ways our ideas confront conventional wisdom. Thus our hypothesis lies in  
494 contrast to the view that fire was controlled first by a relatively late member of the human  
495 lineage, i.e. within the last half-million years, since that idea also necessitates the notion that fire  
496 use had little impact on human evolutionary biology. Likewise it also challenges the idea that  
497 humans are such ecological generalists that they are not adapted to any specific components of  
498 their habitats. Potts exemplified a widely held view: “It is patently incorrect to characterize the  
499 human ancestral environment as a set of specific repetitive elements, statistical regularities, or  
500 uniform problems which the cognitive mechanisms unique to humans are designed to solve” (p.

501 129).<sup>91</sup> By contrast, we claim that humans are biologically adapted to eating cooked food.  
502 Accordingly, the human ancestral environment required the presence of controlled fire and  
503 cooked meals, and thus presented humans with a specific and consistent set of problems relevant  
504 to their biology, behavior and cognition.

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

511

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520

520 **References**

- 521 1 Brace CL. 1995. The Stages of Human Evolution. Englewood Cliffs, NJ: Prentice-Hall.
- 522 2 Burton FD. 2009. Fire: The Spark That Ignited Human Evolution. Albuquerque, NM:  
523 University of New Mexico Press.
- 524 3 Pyke GH. 1984. Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523-  
525 575.
- 526 4 Stephens DW, Krebs JR. 1986. Foraging theory. Princeton, NJ: Princeton University  
527 Press.
- 528 5 Ellison P. 2001. On Fertile Ground. Cambridge, MA: Harvard University Press.
- 529 6 Emery Thompson M, Wrangham RW. 2008. Diet and reproductive function in wild  
530 female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda.  
531 *Am J Phys Anthropol* 135:171-181.
- 532 7 Altmann SA. 1998. Foraging for Survival: Yearling Baboons in Africa. Chicago, IL:  
533 University of Chicago Press.
- 534 8 Lévi-Strauss C. 1970. The Raw and the Cooked. Introduction to a Science of Mythology.  
535 I. New York, NY: Harper Row.
- 536 9 Wrangham R. 2009. Catching Fire: How Cooking Made Us Human. New York, NY:  
537 Basic Books.
- 538 10 Koebnick C, Strassner C, Hoffmann I, Leitzmann C. 1999. Consequences of a long-term  
539 raw food diet on body weight and menstruation: results of a questionnaire survey. *Ann*  
540 *Nutr Metab* 43:69-79.
- 541 11 Carmody RN, Wrangham RW. 2009. The energetic significance of cooking. *J Hum Evol*  
542 57:379–391.

- 543 12 Mason VC. 1984. Metabolism of nitrogenous compounds in the large gut. *P Nutr Soc*  
544 43:45-53.
- 545 13 McNeil NI. 1988. Nutritional implications of human and mammalian large intestinal  
546 function. *World Rev Nutr Diet* 56:1-42.
- 547 14 Livesey G. 1995. The impact of complex carbohydrates on energy balance. *Eur J Clin*  
548 *Nutr* 49:S89-S96.
- 549 15 Silvester KR, Englyst HN, Cummings JH. 1995. Ileal recovery of starch from whole diets  
550 containing resistant starch measured in vitro and fermentation of ileal effluent. *Am J Clin*  
551 *Nutr* 62:403-411.
- 552 16 Oka K, Sakurae A, Fujise T, Yoshimatsu H, Sakata T, Nakata M. 2003. Food texture  
553 differences affect energy metabolism in rats. *J Dent Res* 82:491-494.
- 554 17 McGee H. 2004. *On Food and Cooking: the Science and Lore of the Kitchen*. New York,  
555 NY: Scribner.
- 556 18 Boback SM, Cox CL, Ott BD, Carmody R, Wrangham RW, Secor SM. 2007. Cooking  
557 and grinding reduces the cost of meat digestion. *Comp Biochem Physiol A* 148:651-656.
- 558 19 Aiello LC, Wheeler P. 1995. The expensive tissue hypothesis: the brain and the digestive  
559 system in human and primate evolution. *Curr Anthropol* 36:199-221.
- 560 20 Lucas P. 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge:  
561 Cambridge University Press.
- 562 21 Lucas PW, Ang KY, Sui Z, Agrawal KR, Prinz JF, Dominy NJ. 2006. A brief review of  
563 the recent evolution of the human mouth in physiological and nutritional contexts.  
564 *Physiol Behav* 89:36-38.

- 565 22 James SR. 1989. Hominid use of fire in the Lower and Middle Pleistocene: a review of  
566 the evidence. *Curr Anthropol* 30:1-26.
- 567 23 Preece RC, Gowlett JAJ, Parfitt SA, Bridgland DR, Lewis SG. 2006. Humans in the  
568 Hoxnian: habitat, context and fire use at Beeches Pit, West Stow, Suffolk, UK. *J*  
569 *Quaternary Sci* 21:485-496.
- 570 24 Thieme H. 2005. The Lower Paleolithic art of hunting. In: Gamble CS, Parr M, editors.  
571 *The Hominid Individual in Context: Archaeological Investigations of Lower and Middle*  
572 *Paleolithic Landscapes, Locales and Artefacts*. London: Routledge. p 115-132.
- 573 25 Goren-Inbar N, Alperson N, Kislev ME, Simchoni O, Melamed Y, Ben-Nun A, Werker  
574 E. 2004. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science*  
575 304:725-727.
- 576 26 Sergeant J, Crombé P, Perdaen Y. 2006. The 'invisible' hearths: a contribution to the  
577 discernment of Mesolithic non-structured surface hearths. *J Archaeol Sci* 33:999-1007.
- 578 27 Boback SM. 2006. A morphometric comparison of island and mainland boas (*Boa*  
579 *constrictor*) in Belize. *Copeia* 2006:261-267.
- 580 28 Grant PR, Grant BR. 2002. Unpredictable evolution in a 30-year study of Darwin's  
581 finches. *Science* 296:707-711.
- 582 29 Gould SJ. 2002. *The Structure of Evolutionary Theory*. Cambridge, MA: Harvard  
583 University Press.
- 584 30 Bersaglieri T, Sabeti PC, Patterson N, Vanderploeg T, Schaffner SF, Drake JA, Rhodes  
585 M, Reich DE, Hirschhorn JN. 2004. Genetic signatures of strong recent positive selection  
586 at the lactase gene. *Am J Hum Genet* 74:1111-1120.

- 587 31 Tishkoff SA, Reed FA, Ranciaro A, Voight BF, Babbitt CC, Silverman JS, Powell K,  
588 Mortensen HM, Hirbo JB, Osman M and others. 2007. Convergent adaptation of human  
589 lactase persistence in Africa and Europe. *Nat Genet* 39:31-40.
- 590 32 Perry GH, Dominy NJ, Claw KG, Lee AS, Fiegler H, Redon R, Werner J, Villanea FA,  
591 Mountain JL, Misra R and others. 2007. Diet and the evolution of human amylase gene  
592 copy number variation. *Nat Genet* 39:1256-1260.
- 593 33 Lieberman DE, McBratney BM, Krovitz G. 2002. The evolution and development of  
594 cranial form in *Homo sapiens*. *P Natl Acad Sci* 99:1134-1139.
- 595 34 Lieberman DE, Krovitz GE, Yates FW, Devlin M, Claire MS. 2004. Effects of food  
596 processing on masticatory strain and craniofacial growth in a retrognathic face. *J Hum*  
597 *Evol* 46:655-677.
- 598 35 McHenry HM, Coffing K. 2000. *Australopithecus* to *Homo*: transformations in body and  
599 mind. *Annu Rev Anthropol* 29:125-146.
- 600 36 Wood B, Aiello LC. 1998. Taxonomic and functional implications of mandibular scaling  
601 in early hominins. *Am J Phys Anthropol* 105:523-538.
- 602 37 Jellema LM, Latimer BM, Walker A. 1993. The rib cage. In: Walker A, Leakey R,  
603 editors. *The Nariokotome Homo erectus Skeleton*. Cambridge, MA: Harvard University  
604 Press. p 294-325.
- 605 38 Aiello LC, Wells JCK. 2002. Energetics and the evolution of the genus *Homo*. *Annu Rev*  
606 *Anthropol* 31:323-338.
- 607 39 Bramble DM, Lieberman DE. 2004. Endurance running and the evolution of *Homo*.  
608 *Nature* 432:345-352.

609 40 Aiello LC, Key C. 2002. Energetic consequences of being a *Homo erectus* female. *Am J*  
610 *Hum Biol* 14:551-565.

611 41 Haeusler M, McHenry HM. 2004. Body proportions of *Homo habilis* reviewed. *J Hum*  
612 *Evol* 46:433-465.

613 42 Jungers WL. 1988. Relative joint size and hominoid locomotor adaptations with  
614 implications for the evolution of hominid bipedalism. *J Hum Evol* 17:247-265.

615 43 Walker A, Shipman P. 1996. *The Wisdom of the Bones: In Search of Human Origins*.  
616 New York, NY: Alfred A. Knopf.

617 44 Wood BA, Collard M. 1999. The human genus. *Science* 284:65-71.

618 45 Werdelin L, Lewis ME. 2005. Plio-Pleistocene Carnivora of eastern Africa: species  
619 richness and turnover patterns. *Zool J Linn Soc* 144:121–144.

620 46 Sabater Pi J, Veà JJ, Serrallonga J. 1997. Did the first hominids build nests? *Curr*  
621 *Anthropol* 38:914-16.

622 47 Anderson JR. 2000. Sleep-related behavioural adaptations in free-ranging anthropoid  
623 primates. *Sleep Med Rev* 4:355-373.

624 48 Medawar PB. 1952. *An Unsolved Problem of Biology*. London: H. K. Lewis.

625 49 Williams GC. 1957. Pleiotropy, natural selection, and the evolution of senescence.  
626 *Evolution* 11:398-411.

627 50 Austad SN. 1993. Retarded senescence in an insular population of Virginia opossums  
628 (*Didelphis virginiana*). *J Zool (Lond)* 229:695–708.

629 51 Harvey PH, Zammuto RM. 1985. Patterns of mortality and age at first reproduction in  
630 natural populations of mammals. *Nature* 315:319-320.

- 631 52 Promislow DEL, Harvey PH. 1990. Living fast and dying young: a comparative analysis  
632 of life-history variation among mammals. *J Zool (Lond)* 220:417–437.
- 633 53 Luckinbill LS, Clare M. 1985. Selection for life span in *Drosophila melanogaster*.  
634 *Heredity* 55:9-18.
- 635 54 Ricklefs RE. 1998. Evolutionary theories of aging: confirmation of a fundamental  
636 prediction, with implications for the genetic basis and evolution of life span. *Am Nat*  
637 152:24-44.
- 638 55 Rose M, Charlesworth B. 1981. Genetics of life history in *Drosophila melanogaster*. II.  
639 Exploratory selection experiments. *Genetics* 97:187–196.
- 640 56 Charnov EL, Berrigan D. 1993. Why do female primates have such long lifespans and so  
641 few babies? or life in the slow lane. *Evol Anthropol* 1:191-194.
- 642 57 Dean CM, Smith BH. 2009. Growth and development of the Nariokotome youth, KNM-  
643 WT 15000. In: Grine FE, Fleagle JG, Leakey RE, editors. *The first humans: origin and*  
644 *early evolution of the genus Homo*. New York, NY: Springer. p 101–120.
- 645 58 Kaplan HS, Hill K, Lancaster JB, Hurtado AM. 2000. A theory of human life history  
646 evolution: diet, intelligence and longevity. *Evol Anthropol* 9:156-183.
- 647 59 Robson SL, Wood B. 2008. Hominin life history: reconstruction and evolution. *J Anat*  
648 212:394–425.
- 649 60 Hawkes K, O’Connell JF, Blurton Jones NG, Alvarez H, Charnov EL. 1998.  
650 Grandmothering, menopause and the evolution of human life history strategies. *P Natl*  
651 *Acad Sci* 95:1336–1339.
- 652 61 Kramer KL. 2005. Children's help and the pace of reproduction: cooperative breeding in  
653 humans. *Evol Anthropol* 14:224-237.



- 654 62 Robson SL, van Schaik C, Hawkes K. 2006. The derived features of human life history.  
655 In: Paine RL, Hawkes K, editors. *The Evolution of Human Life History*. Santa Fe, NM:  
656 School of American Research Press. p 17-44.
- 657 63 Shattuck MR, Williams SA. 2010. Arboreality has allowed for the evolution of increased  
658 longevity in mammals. *P Natl Acad Sci* 107:4635-4639.
- 659 64 Stewart OC. 1958. Fire as the first great force employed by man. In: Thomas WL, editor.  
660 *Man's Role in Changing the Face of the Earth*. Chicago, IL: University of Chicago Press.  
661 p 115-133.
- 662 65 Demas GE. 2004. The energetics of immunity: a neuroendocrine link between energy  
663 balance and immune function. *Horm Behav* 45:173-180.
- 664 66 Nagao M. 1992. The effects of aging on mastication. *Nutr Rev* 50:434-437.
- 665 67 Tzakis MG, Österberg T, Carlsson GE. 1994. A study of some masticatory functions in  
666 90-year old subjects. *Gerodontology* 11:25-29.
- 667 68 Newton JP, Yemm R, Abel RW, Menhinick S. 1993. Changes in human jaw muscles  
668 with age and dental state. *Gerodontology* 10:16-22.
- 669 69 Nakanishi N, Fukuda H, Takatorige T, Tatara K. 2005. Relationship between self-  
670 assessed masticatory disability and 9-year mortality in a cohort of community-residing  
671 elderly people. *J Am Geriatr Soc* 53:54-58.
- 672 70 Semba RD, Blaum CS, Bartali B, Xue QL, Ricks MO, Guralnik JM, Fried LP. 2006.  
673 Denture use, malnutrition, frailty, and mortality among older women living in the  
674 community. *J Nutr Health Aging* 10:161-167.

675 71 Black RE, Lopez de Romaña G, Brown KH, Bravo N, Grados Bazalar O, Creed  
676 Kanashiro H. 1989. Incidence and etiology of infantile diarrhea and major routes of  
677 transmission in Huascar, Peru. *Am J Epidemiol* 129:785-799.

678 72 Rowland MGM, Barrell RAE, Whitehead RG. 1978. The weanling's dilemma: bacterial  
679 contamination in traditional Gambian weaning foods. *Lancet* 1:136-138.

680 73 Brown KH, Bégin F. 1993. Malnutrition among weanlings of developing countries. still a  
681 problem begging for solutions. *J Pediatr Gastr Nutr* 17:132-138.

682 74 Ellison PT. 2003. Energetics and reproductive effort. *Am J Hum Biol* 15:342-351.

683 75 Ford K, Huffman SL, Chowdhury AKMA, Becker S, Allen H, Menken J. 1989. Birth-  
684 interval dynamics in rural Bangladesh and maternal weight. *Demography* 26:425-437.

685 76 Huffman SL, Ford KT, Allen HA, Streble P. 1987. Nutrition and fertility in Bangladesh:  
686 breastfeeding and post partum amenorrhoea. *Pop Stud* 41:447-462.

687 77 O'Connell JF, Hawkes K, Blurton Jones NG. 1999. Grandmothering and the evolution of  
688 *Homo erectus*. *J Hum Evol* 36:461-485.

689 78 Martin RD, Chivers DJ, MacLarnon AM, Hladik CM. 1985. Gastrointestinal allometry in  
690 primates and other mammals. In: Jungers WL, editor. *Size and Scaling in Primate*  
691 *Biology*. New York, NY: Plenum Press. p 61-89.

692 79 Milton K, Demment MW. 1988. Chimpanzees fed high and low fiber diets and  
693 comparison with human data. *J Nutr* 118:1082-1088.

694 80 Stedman HH, Kozyak BW, Nelson A, Thesier DM, Su LT, Low DW, Bridges CR,  
695 Shrager JB, Minugh-Purvis N, Mitchell MA. 2004. Myosin gene mutation correlates with  
696 anatomical changes in the human lineage. *Nature* 428:415-418.

- 697 81 Barton RA. 1992. Allometry of food intake in free-ranging anthropoid primates. *Folia*  
698 *Primatol* 58:56-59.
- 699 82 Leonard WR, Robertson ML. 1997. Comparative primate energetics and hominid  
700 evolution. *Am J Phys Anthropol* 102:265-281.
- 701 83 Isler K, van Schaik CP. 2006. Costs of encephalization: the energy trade-off hypothesis  
702 tested on birds. *J Hum Evol* 51:228-243.
- 703 84 Pagel M, Bodmer W. 2003. A naked ape would have fewer parasites. *P R Soc London*  
704 270:S117-S119.
- 705 85 Wheeler P. 1992. The influence of the loss of functional body hair on hominid energy  
706 and water budgets. *J Hum Evol* 23:379-388.
- 707 86 Rantala MJ. 2007. Evolution of nakedness in *Homo sapiens*. *J Zool (Lond)* 273:1-7.
- 708 87 Kuzawa CW. 1998. Adipose tissue in human infancy and childhood: an evolutionary  
709 perspective. *Yearb Phys Anthropol* 41:177-209.
- 710 88 Shipman P, Walker A. 1989. The costs of becoming a predator. *J Hum Evol* 18:373-392.
- 711 89 Marlowe FW. 2005. Hunter-gatherers and human evolution. *Evol Anthropol* 14:54-67.
- 712 90 Wobber V, Hare B, Wrangham R. 2008. Great apes prefer cooked food. *J Hum Evol*  
713 55:340-348.
- 714 91 Potts R. 1998. Environmental hypotheses of hominin evolution. *Yearb Phys Anthropol*  
715 41:93-138.
- 716 92 Harvey PH, Martin RD, Clutton-Brock TH. 1987. Life histories in comparative  
717 perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT,  
718 editors. *Primate Societies*. Chicago, IL: University of Chicago Press. p 181-196.

- 719 93 Charnov EL. 1991. Evolution of life history variation among female mammals. *P Natl*  
720 *Acad Sci* 88:1134-1137.
- 721 94 Charnov EL, Berrigan D. 1990. Dimensionless numbers and life history evolution: age of  
722 maturity versus the adult lifespan. *Evol Ecol* 4:273-275.
- 723 95 Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain NL. 1999. The raw and  
724 the stolen: cooking and the ecology of human origins. *Curr Anthropol* 40:567-594.
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727 **Figures**

728

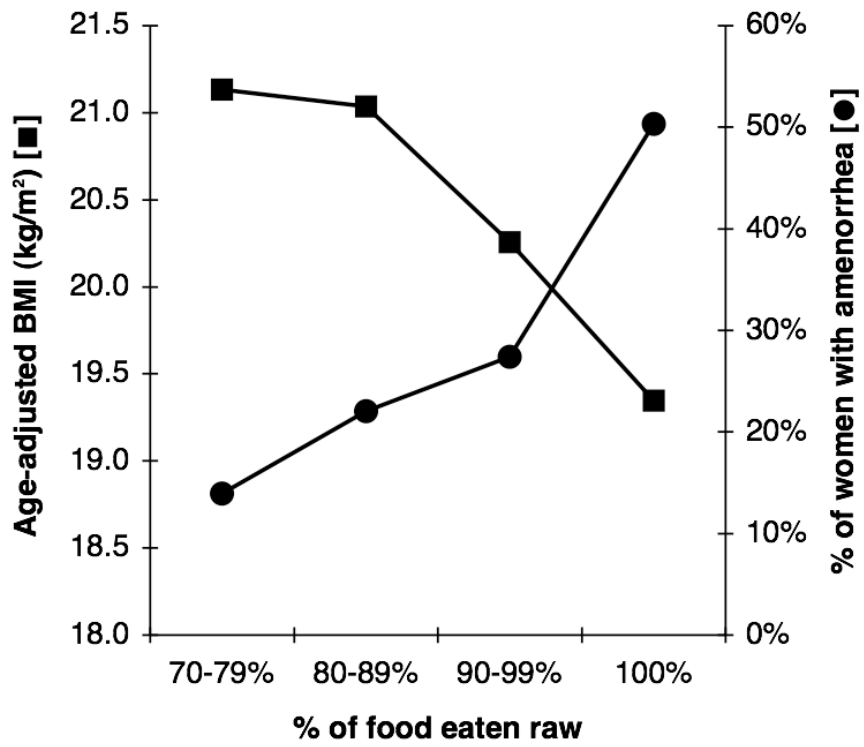
729 **Figure 1.**



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731 **Figure 2.**

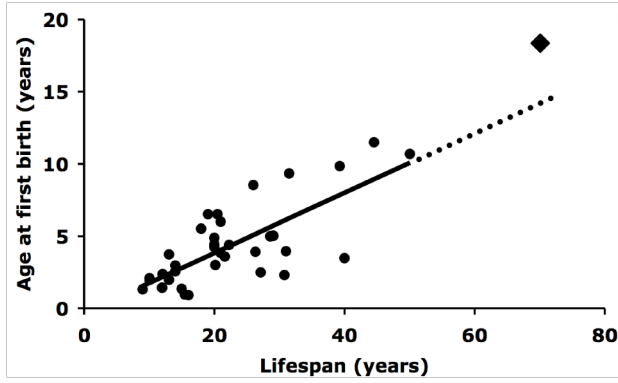


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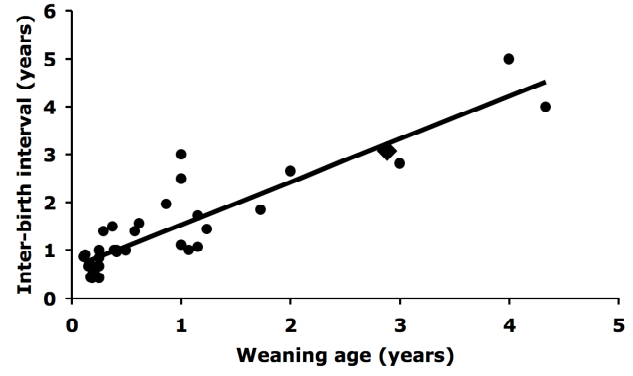
733 **Figure 3.**

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3a.



3b.



3c.



3d.

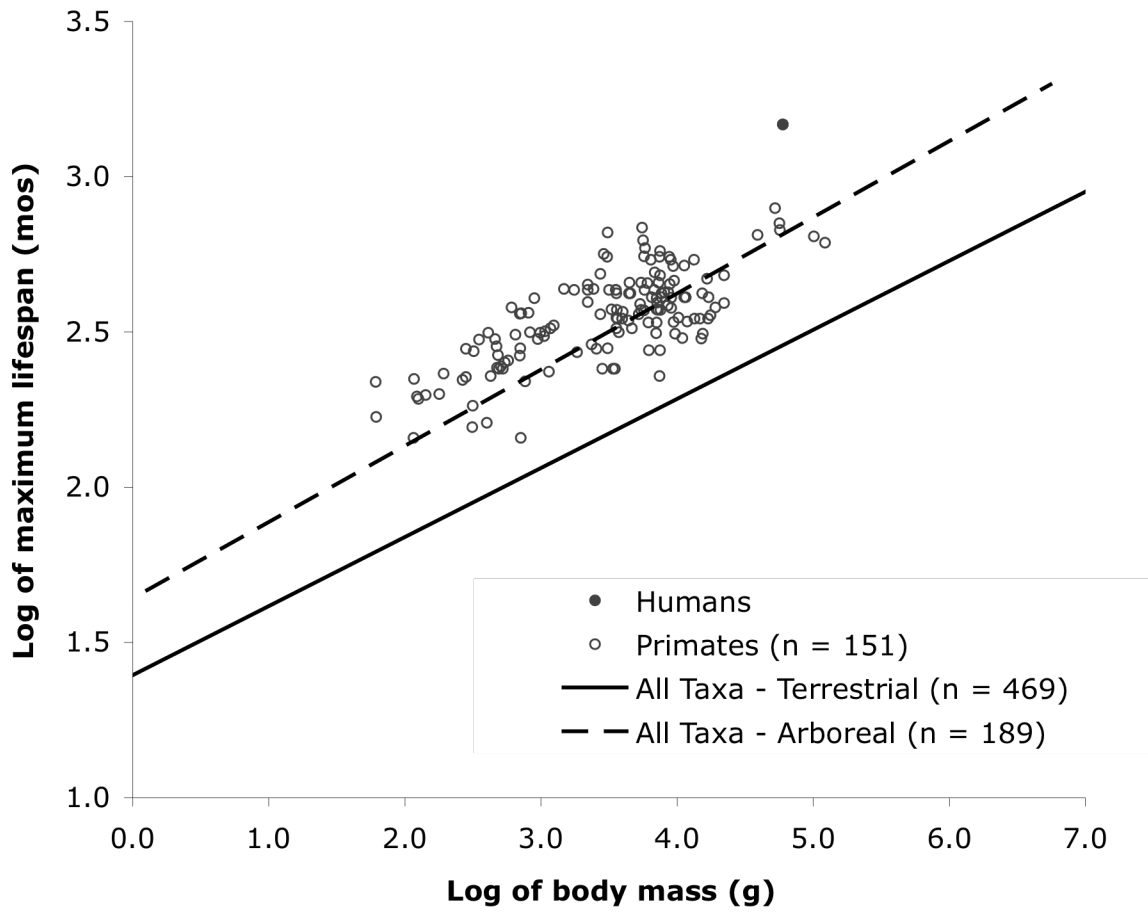


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736 **Figure 4.**

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739 **Figure Legends**

740

741 **Figure 1.** Baboon being prepared for cooking in a Hadza camp, northern Tanzania. Following a  
742 widespread practice, the hunters have laid the prey on the fire in order to remove the hair by  
743 singeing. After the hair has gone they sometimes leave the carcass on the fire and let it roast in  
744 situ. Alternatively they boil the meat in a pot. Photograph and information courtesy of Frank W.  
745 Marlowe.

746

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

752

753 **Figure 3.** The human life history puzzle. In most species different life history parameters are  
754 consistent in their pace, as illustrated here for non-human primate species (solid circles) by  
755 correlations among four life history variables. Unusually, hunter-gatherers (large diamond) are  
756 slow in two variables (lifespan, age at first birth), but fast in two others (weaning, inter-birth  
757 interval). Figure 3a: non-human primates with long maximum lifespan tend to have late age of  
758 first birth ( $r^2 = 0.56$ ,  $n = 36$ ,  $p < 0.001$ ). Humans are here assigned a conservative estimate of 70  
759 years for maximum lifespan, following Harvey and colleagues,<sup>92</sup> and fall close to the primate  
760 line. Figure 3b: non-human primates with later weaning have longer inter-birth intervals ( $r^2 =$   
761  $0.80$ ,  $n = 36$ ,  $p < 0.001$ ). Hunter-gatherers conform to the primate trend. Figure 3c: non-human

762 primates with a late age of first birth tend to have long inter-birth intervals ( $r^2 = 0.61$ ,  $n = 41$ ,  $p <$   
763  $0.001$ ); however hunter-gatherers have shorter inter-birth intervals than expected. Figure 3d:  
764 non-human primates with a late age of first birth tend to wean later ( $r^2 = 0.82$ ,  $n = 29$ ,  $p < 0.001$ ),  
765 but hunter-gatherers have an earlier weaning age than expected. The puzzle about humans is why  
766 they combine fast reproduction (short inter-birth interval and early weaning) with slow growth  
767 (late age at first birth). Data sources: non-human primates, Harvey and colleagues<sup>92</sup>; hunter-  
768 gatherers, Marlowe<sup>89</sup> (Table 2, warm-climate, non-equestrian only). Number of hunter-gatherer  
769 societies contributing to mean values: age at first birth, 6; inter-birth interval, 9; weaning age, 18.

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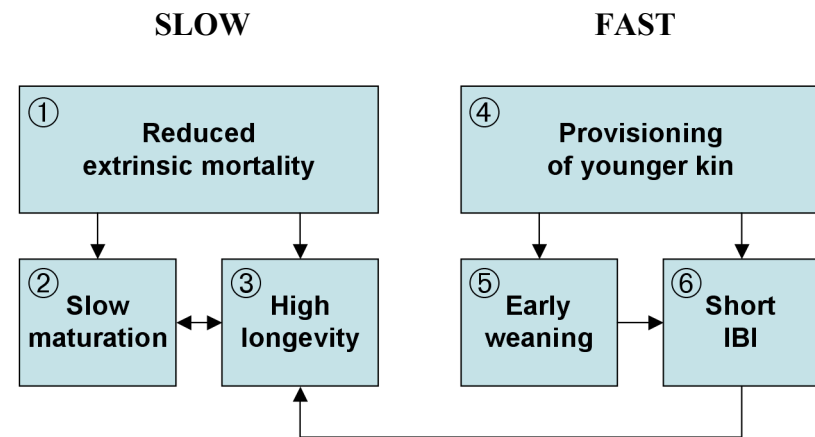
771 **Figure 4.** Maximal lifespan plotted against body mass for humans (closed circle) and 151  
772 primates (open circles), compared to the ordinary least squares regressions for 189 arboreal  
773 mammals (dashed line:  $0.25x + 1.64$ ,  $r^2 = 0.50$ ,  $p < 0.001$ ) and 469 terrestrial mammals ( $y =$   
774  $0.22x + 1.39$ ,  $r^2 = 0.76$ ,  $P < 0.001$ ). Modified from Figure 2 in Ref. 63 using data provided by  
775 Shattuck and Williams.

## Text Box

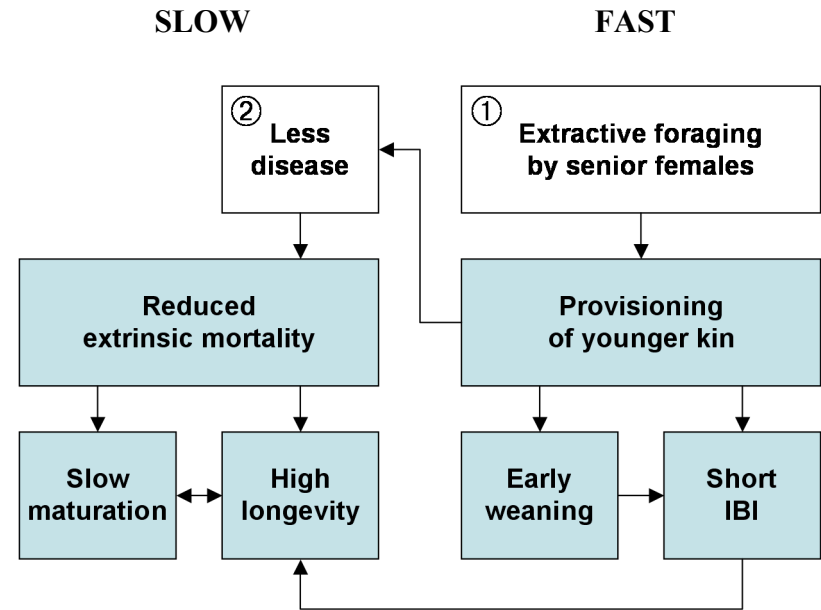
**Box 1.** Summaries of three solutions to the human life history paradox: (1) the “grandmother hypothesis”;<sup>60</sup> (2) the “embodied capital model”;<sup>58</sup> and (3) the “control-of-fire hypothesis”. The three solutions are not mutually exclusive.

**Common framework.** 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 ( $\alpha$ ) is expected under Charnov’s dimensionless approach to life history, in which  $\alpha M$  is approximately constant across related taxa.<sup>93</sup> Slow maturation, in turn, promotes increased adult body mass.\* Reduced extrinsic mortality will also favor increased longevity, as the average adult lifespan is roughly  $1/M$ .<sup>94</sup> 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 post-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.

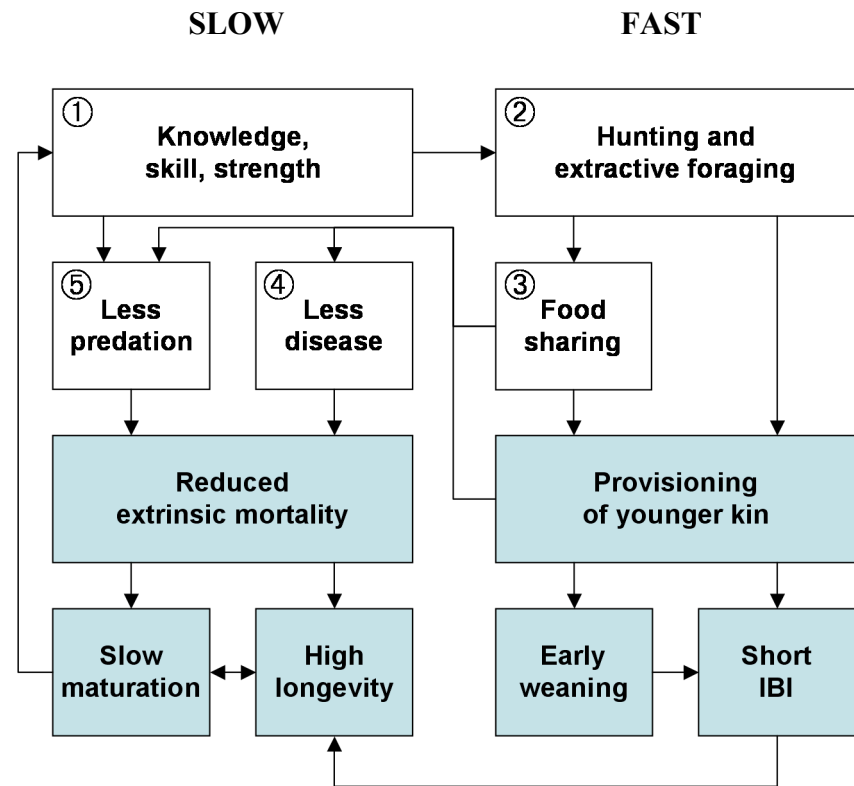
\* Body mass increase in *Homo* is complicated by a reduction in sexual dimorphism, so that only females experience the increased mass. Reduction in sexual dimorphism in *Homo* is thought to be due to sexual selection,<sup>95</sup> which we do not discuss in the present paper.



**Grandmother hypothesis.**<sup>60</sup> 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 post-reproductive 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 childcare, allows for higher fertility of reproductive-aged kin. Since inclusive fitness rises for post-reproductive women who provision, ‘long-lived helper’ genes increase in frequency in the gene pool, contributing to longevity. In addition, continued provisioning by post-reproductive women lowers the susceptibility to disease [2] of juvenile kin, further selecting for increased longevity. Hawkes and colleagues argue that these relationships may explain the evolution of postmenopausal longevity in humans.<sup>60</sup> The complementarity between the grandmother hypothesis and the control-of-fire hypothesis is illustrated by the fact that O’Connell and colleagues discussed the importance of cooking as a mechanism that helped enable provisioning of kin.<sup>77</sup>



**Embodied capital model.**<sup>58</sup> 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] that 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 non-kin-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 it allows for 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 non-linearly with longevity. Kaplan and colleagues argue that these relationships lead to co-evolution between the human patterns of life history and extreme intelligence.<sup>58</sup>



**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 for 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.<sup>10</sup> 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 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. 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 a stable nutritional status as a result of a high-quality cooked diet and a culture of provisioning, 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. Finally, 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.

