

Review

‘Cooking as a biological trait’[☆]

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Abstract

No human foragers have been recorded as living without cooking, and people who choose a ‘raw-foodist’ life-style experience low energy and impaired reproductive function. This suggests that cooking may be obligatory for humans. The possibility that cooking is obligatory is supported by calculations suggesting that a diet of raw food could not supply sufficient calories for a normal hunter–gatherer lifestyle. In particular, many plant foods are too fiber-rich when raw, while most raw meat appears too tough to allow easy chewing. If cooking is indeed obligatory for humans but not for other apes, this means that human biology must have adapted to the ingestion of cooked food (i.e. food that is tender and low in fiber) in ways that no longer allow efficient processing of raw foods. Cooking has been practiced for ample time to allow the evolution of such adaptations. Digestive adaptations have not been investigated in detail but may include small teeth, small hind-guts, large small intestines, a fast gut passage rate, and possibly reduced ability to detoxify. The adoption of cooking can also be expected to have had far-reaching effects on such aspects of human biology as life-history, social behavior, and evolutionary psychology. Since dietary adaptations are central to understanding species evolution, cooking appears to have been a key feature of the environment of human evolutionary adaptedness. Further investigation is therefore needed of the ways in which human digestive physiology is constrained by the need for food of relatively high caloric density compared to other great apes.

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1. Introduction

At least four biologically significant differences are widely recognized between the diets of hunter–gatherers and other great apes. First, humans eat more meat than chimpanzees (and other apes) (e.g. Milton, 1987; Kelly, 1995; Cordain et al., 2000; Mann, 2000). Second, roots are more impor-

tant in forager diets than they are for other apes (Hatley and Kappelman, 1980; O’Connell et al., 1999; Conklin-Brittain et al., 2002; Laden and Wrangham, in press). Third, although humans are generalists capable of eating a wide range of items (Potts, 1998; Teaford et al., 2002), at any one time foraging populations tend to specialize on a narrow diet breadth (Blurton-Jones et al., 1999). Fourth, humans employ a variety of novel food-processing techniques that improve food quality in various ways, including elevating energy density and reducing toxins (Stahl, 1984; Ragir, 2000; Milton, 2002; Teaford et al., 2002). These four traits are thought to reflect an evolutionary commitment to a diet of relatively high-calorie items compared to

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the fruits and foliage that dominate the diets of great apes.

Here we propose that cooking represents a fifth important feature of the human diet. Normally cooking is regarded as too novel to have had evolutionary significance. In contrast to that view, we propose that as a result of a long history of cooking, adaptation has occurred in various human traits concerned both with digestion and with other biological features (cf. Brace et al., 1987; Brace, 1995; Wrangham et al., 1999; Wrangham, 2001). However, much remains to be discovered about how humans have adapted biologically to cooking.

2. The distribution of cooking

We define cooking as applying heat to improve the nutritional quality of food. According to this definition, it is normally claimed that all human populations cook (e.g. Harris, 1992). We have searched the literature for challenges to this generalization, not only among farmers and hunter-gathers but also for cases of explorers, adventurers, or warriors. Among contemporary agricultural populations, ‘raw-foodist’ individuals sometimes choose to fore-go cooked food for years at a time (below). Other than these deliberate raw-foodists, we have not found any current or historical examples of individuals or small groups living for more than a few days without access to cooked foods. Contrary to earlier speculation, all recorded hunter-gatherers have known how to make fire (Gott, 2002).

Perhaps the most notable inclusion of raw meat in forager diets was by unacculturated Inuit peoples of Canada and Alaska. The Inuit represent one of the most recently adopted human lifestyles, approximately 4000 years old (Smith, 1991). When the explorer Stefansson became the first Westerner to live with unacculturated Inuit, raw blubber was a frequent item of their diet and was reported to be preferred to cooked blubber by at least some people (Stefansson, 1913). Cuts of seal-meat and fish could also be eaten raw. But meat, blubber and even blood were sometimes cooked. The ambiguous nature of the evidence is shown by the fact that out of four reports of early contacts with Inuit (1881–1913), three reported that food was generally cooked, while the fourth claimed that food was generally eaten raw (Stefansson, 1960). In the absence of quantitative data, we conclude that cooking may have been less

important for Arctic hunters than in most societies, but that it was nevertheless practiced regularly. Raw meat may have been specially important in Inuit diets by providing vitamin C, which is normally provided by plant diets (Draper, 1977).

Lists of plant foods in hunter-gatherer diets typically include many items that can be eaten raw. For example, Laden and Wrangham (in press) reported that 56% of 48 plant roots eaten by African foragers were sometimes eaten raw. But such items tend to provide snacks rather than meals. More importantly, hunter-gatherers typically cook at least one meal every day, normally in the late afternoon or early evening, whereas snacks during the day are more likely to be eaten raw (e.g. O’Dea, 1991).

Thus no human populations are known to have lived without regular access to cooked food.

3. The antiquity of cooking

Despite much discussion about the role of fire in human evolution (e.g. James, 1989; Straus, 1989; Goudsblom, 1992), cooking is often viewed as irrelevant to human evolutionary biology. Thus, in many texts about the evolution of humans or their food habits, cooking is not discussed at all (e.g. human evolution: Lewin, 1993; Boaz and Almquist, 1997; Relethford, 1997; Boyd and Silk, 2000; evolution of human food habits: Ortner, 1983; Harris and Ross, 1987; Ungar and Teaford, 2002). In other cases it is mentioned only briefly (e.g. Jurmain and Nelson, 1994; Park, 1996). It is rarely featured prominently (Brace, 1995), and even authors writing explicitly about the need to understand ‘the nutrition for which human beings are in essence genetically programmed’ have entirely failed to discuss it (Eaton and Konner, 1985, p. 283).

The reason why cooking is ignored in this way appears to be the widespread assumption that it has been practiced for too short a time to have had any impact on biological evolution. Here is a typical claim: ‘Once *Homo sapiens* became established as a distinct omnivorous species, surviving by hunting and gathering, there is no reason to believe that further *biological* evolution occurred in man’s nutrient needs’ (Scrimshaw (1983, p. 229). Implicit in Scrimshaw’s remark is the notion that the adoption of hunting and gathering long preceded cooking. Milton (2002) was more specific. She considered that ‘relatively recent changes

in certain features of the modern human diet (e.g. cooking of most foods, ...) may, in an evolutionary sense, have occurred so rapidly and so recently that human biology has not yet had time to adapt to them' (Milton, 2002, p. 112).

Current evidence, however, does not support the notion of cooking as being too recent to have had evolutionary effects. The typical duration of a speciation event is considered to be 15 000–25 000 years, and mammalian species can evolve in as little as 5000 years (Gould, 2002). Human biology is also known to be capable of rapid adaptation (e.g. to malaria, Durham, 1991) and specifically in response to a change in diet. Thus populations with a high frequency of genes responsible for lactose absorption (LA) in adults are those with a history of dairying. Populations are estimated to have adapted biologically to milk-drinking in 5000 years or less (i.e. LA genes increased from 5 to 70% of population, Aoki, 1991; Cavalli-Sforza et al., 1994). These points suggest that for cooking to have been practiced too recently to have had evolutionary effects, it must have been adopted less than 5000 years ago.

But cooking is undoubtedly older than 5000 years. For example it is necessary for the processing of cereal grains, which were being harvested 20 000 years ago by people skilled in fire management and grinding (Brooks, 1996; Bar-Yosef, 2001). Previous to grain-eating, the pattern of food preparation by Neandertals appeared essentially modern in Kebara Cave, Israel throughout the period from 60 000 to 48 000 years ago (Speth and Tchernov, 2001). Large numbers of bones were burned there, similar to patterns in a New Mexico village around 1300 AD.

Further back in time, various European and Middle Eastern sites that go back more than 250 000 years ago contain extensive evidence of hominid use of fire (James, 1989). Brace and his colleagues have emphasized the importance of apparent 'earth-ovens' from these sites (e.g. Brace et al., 1987; Brace, 1995, 1996, 1999). They conclude 'that the application of heat to food, if for no other purposes than to thaw the frozen remainders of yesterday's haunch, made an important contribution to subsistence at the northern edges of human occupation' (Brace, 1999, p. 256). Cooking is therefore widely accepted back to at least 250 000 years ago (Ragir, 2000).

Other evidence points to the control of fire by hominids even earlier, such as 400 000–600 000

years ago in Vértesszölös, Hungary (Kretzoi and Dobosi, 1990), more than 1 million years ago in Swartkrans, South Africa (Brain, 1993), and 1.6 million years ago at Koobi Fora, Kenya (Rowlett, 2000) (see Straus, 1989). The oldest date suggested for the adoption of cooking is 1.9 million years ago (Wrangham et al., 1999), a time that marks the origin of the modern human body form (*Homo ergaster*), a rise in dietary quality, and a shift towards a human pattern of life-history (Leonard and Robertson, 1997; Aiello and Key, 2002; O'Connell et al., 2002). The hypothesis of such an early date for the adoption of cooking is inferred from biological evidence, and awaits archeological scrutiny (Brace, 2002). Thus the precise date when cooking was adopted is unknown. Nevertheless, cooking is clearly ancient compared to the time required for biological adaptation to occur.

Brace et al. (1987) hypothesized that because people could not have survived winters without being able to de-frost meat from kills, cooking became obligatory for hominids occupying glacial zones, 250 000 years ago (Brace, 1995). Here we extend their suggestion that frozen-meat-cooking is obligatory by suggesting that without the use of cooking, most plant foods are not sufficiently digestible, and most meat foods are not sufficiently tender. We first consider the effects of a raw-food diet.

4. Effects of a raw-food diet

In the only research that we have found of the effects of a raw-food diet, Koebnick et al. (1999) studied urban Germans who preferred their food raw. They believed that a raw-food diet was morally sound or had health benefits (e.g. preventing illness, promoting long life, reducing allergies, and reducing the risk of being overweight). Some of the raw-foodists were vegetarians, while others included raw meat in their diet.

Raw-foodists in this study survived largely on raw food for 3 years or more, though most (82%) preferred to supplement their diets with small amounts of cooked foods. They had access to shops containing a wide range of domesticated foods from around the world. Even eating these high-quality diets, raw-foodists were vulnerable to energy shortage. Thus of the 18% that followed a 100% raw-food diet, 31% were judged to suffer from Chronic Energy Deficiency. The negative effect of an inadequate energy supply was indicat-

ed by women's reproductive performance, which worsened steadily with larger amounts of raw food. Thus among women on 100% raw-food diets, approximately 50% of women were completely amenorrheic, while a further proportion (not reported) suffered irregular and/or incompetent menstrual cycles. Although this could in theory result from vegetarianism, current data indicate that weight-stable vegetarian women have fewer menstrual disturbances than non-vegetarians (Barr, 1999). Koebnick et al. (1999, p. 77) concluded that energy shortage was the problem, and that 'a strict raw food diet cannot guarantee an adequate energy supply'.

Since Koebnick et al.'s data were from a well-fed population with low activity levels compared to hunter-gatherers, and with access to high-quality agricultural foods year-round, their conclusion raises the question of whether people could survive on a raw food diet in the wild.

5. Theoretical problems with a raw diet

5.1. Plants

Wrangham et al. (1999) noted five ways in which foods are improved or softened by cooking. It can break down physical barriers such as thick skins or husks by softening the cellulose present (Bender, 1982; Birch et al., 1986). It can burst cells, also helped by cellulose softening, making cell contents more easily available for digestion or absorption. It can modify the physical structure of molecules such as proteins and starches, into forms more accessible for digestion by enzymatic degradation (see below). It can reduce the chemical structure of indigestible molecules into smaller forms that can be fermented more rapidly and completely (Smith et al., 2001). Finally, it can denature toxins or digestion-reducing compounds (Stahl, 1984). In their different ways, each of these mechanisms makes food more available, either rendering it palatable or raising its digestibility (defined as the proportion of dry matter intake not present in the feces).

Modifying the physical structure of macromolecules such as proteins and starches often makes them more accessible to enzymatic digestion. Most types of cooking tend to increase the digestibility of starch, for example (Holm et al., 1988; Kataria and Chauhan, 1988; Ayankunbi et al., 1991; Muir and O'Dea, 1992; Yiu, 1993; Kingman and

Englyst, 1994; Ruales and Nair, 1994; Urooj and Puttaraj, 1994; Barampama and Simard, 1995; Periago et al., 1996; Bravo et al., 1998; Marconi et al., 2000; Sagum and Arcot, 2000; Slavin et al., 2001; Smith et al., 2001). The same is true of plant protein digestibility (Rao, 1996; Chitra et al., 1996; Khalil, 2001).

The effects of cooking on the plant fiber fractions is perhaps even more important. The fiber content and texture influences palatability as well as the rate at which the teeth can process a given food. Even an insoluble fiber such as cellulose will soften in the presence of heat and water. There is also evidence that with dry heat insoluble fiber is converted into soluble fiber (Phillips and Palmer, 1991; Muir and O'Dea, 1992; Veena et al., 1995; Periago et al., 1997; Bravo, 1999). This conversion to softer fibers, as well as the gelatinization of starch due to the heat, results in the cells separating more easily and the plant food becoming easier to bite and chew (Birch et al., 1986). This changes the rate of energy intake per minute of eating, and hence the likely rate at which energy can be gained per day.

The method of preparation, and the specific item, affects the impact of cooking on nutrient digestibility (Trout et al., 1993). The cooking methods used in the publications cited above included not only baking but also roasting, boiling, pressure-cooking, autoclaving, and extrusion cooking. Although most of these are too recent to be relevant to human evolutionary biology, the largest impact was for any kind of cooking compared to raw food. Similarly these investigations included not only vegetables, but also grains and legumes. The hypothesis that cooking wild plant foods would have improved their nutritional value is thus supported by the general trends, but data are still required to quantify the effect using relevant foods and relevant methods of cooking.

Continuing this comparison between raw and cooked food, and returning to the effects of a raw food diet seen among modern raw-foodists, Koebnick et al. (1999) did not speculate on the cause of the energy shortage they observed. However, using Zootrition, 2.0 Software (2002) to calculate raw food diets and Fuel, 2.3 Nutrition Software (2000) to calculate conventional, modern human diets, we suggest that it would be difficult for a woman on a raw food diet to consume enough energy to maintain a regular menstrual cycle. We assume that she weighs 54.5 kg (120 lbs), and

Table 1

A modern raw foodist diet for a 120-lb (54.7 kg), 5 foot 4 inches (160 cm) adult woman consuming a 2000-kcal (8368-kJ) diet (Zootrition, 2.0 Software, 2002), compared to two estimated raw food diets for the same individual, corrected to 80% water and 33% NDF

Diet content	Fresh wt. (g)	% of BW	Dry wt. (g)	Water (g)	Fat %DM	Protein %DM	NDF %DM
10 Fruit, 10 vegetables 5 greens	5000	9.2	597.4	4402.6	2.6	14.0	8.5
Fruits and leaves, corrected	4145.5	7.6	829.1	3316.4	2.6	14.0	33
Fruits, leaves, and raw meat, corrected	2951.4	5.4	590.3	2361.1	2.6	27.4	30.2

DM, dry matter; NDF, neutral-detergent fiber (total insoluble fiber); BW, body wt.

needs, 2000 kcal (8368 kJ) (Table 1) to support a sedentary lifestyle of sleeping, eating, driving, reading, cooking, and some level ground walking. If she ate equal amounts of 10 types of fruits, 10 succulent vegetables and five types of greens commonly available in supermarkets, she would have to eat 200 g of each every day to obtain 2000 kcal and a protein level of 14%. This 5 kg of fresh food represents 9.2% of her body weight, not including beverages. This is a larger daily weight of food than normally recorded for humans, which raises the possibility that it is unsustainably high (cf. Milton, 2002). Unfortunately this hypothesis is difficult to test because the literature on human gut capacity is contradictory and incomplete.

This diet also contains a fiber content of 51 g dry wt. (423 g fresh wt.). This level slightly surpasses the fiber amount reported for non-westernized, cooking people (40 g, Conklin-Brittain et al., 2002) and is approximately twice as high as the recommended level for western diets (Butrum et al., 1988). Higher amounts of fiber can elevate passage rate, so our model diet would be expected to generate a higher passage rate compared to a cooked-food-eater. Accordingly, this might reduce the amounts of nutrients the gut can absorb from food as it passes through. However, there have been no controlled experiments to determine the upper levels of fiber to which humans can adapt.

Five kg of daily food is clearly high. For example, on a cooked, western diet (targeting 30% fat, 15% protein), our same sedentary female would need to consume 3.5% of her body wt./day

or 1.92 kg of food to obtain 2000 kcal. This represents only 38% of the weight that she was consuming above. Even during the course of Thanksgiving Day, when it is not unusual for Americans to consume 7000 kcal (29 288 kJ) of cooked, western diet, the total intake would be 4.6 kg, i.e. only 91% of the raw-foodist's daily intake.

To suggest what these calculations would imply for the diet of a pre-cooking hunter-gatherer woman, the nature of her foods must be taken into account. Wild fruits and vegetables have less water and more fiber than their domestic equivalents. Table 1 therefore shows an estimated diet for a raw-foodist hunter-gatherer based on drier, more fibrous foods than for modern raw-foodists. The raw-foodist hunter-gatherer female would have had to consume foods totaling only 7.6% of her body weight daily (Table 1), but she would also have been obliged to chew and ingest almost five times as much raw fiber (274 g dry wt., 1.37 kg fresh wt.) per day compared to the modern raw-foodist. There is no evidence that humans could survive on such a high fiber intake, and we tentatively suggest that it is not possible in view of the adaptations of humans for diets of high caloric density (Milton, 2000, 2002).

These calculations assume an all-plant diet, so they are not realistic because hunter-gatherers would have included meat in their diet. If we substitute 250 g of raw, ground venison (at 2.4% fat) for an equivalent amount of plant material in the above raw, wild plant diet, the pre-cooking, hunter-gatherer would have had to consume only 5.4% of her body weight to satisfy daily (seden-

tary) energy requirements (Table 1). Thus it would appear that adding meat would substantially improve energy intake. However, she would still have been consuming 2.7 kg of raw vegetable matter containing approximately 178 g of fiber (890 g fresh wt.) per day. To compound the problem, it appears that raw and unground meat cannot be chewed at a satisfactory rate (see below). These points suggest that a raw-food diet would present constraints of time and energy for a hunter–gatherer.

5.2. Meat

The factors normally considered to constrain meat-eating by hunter–gatherers are the costs of obtaining it and preparing it to be eaten (hunting, scavenging, and cutting with stone flakes, Stanford and Bunn, 2001). Such problems are not significantly aided by cooking. Likewise the digestibility of meat (up to 100%) is not much affected by cooking. For these reasons little attention has been paid to the possible importance of cooking in facilitating meat-eating for humans. Instead, the relevance of cooking for the evolutionary significance of meat-eating has been discussed largely with respect to the special context of its value in de-frosting large kills (Brace, 1995).

However, it has also been suggested that the most significant effect of cooking on meat-eating is tenderizing, because this allows a high rate of intake (e.g. Coon, 1954). The meat of wild tropical and temperate mammals is generally low in fat and rich in collagen, making it tough to chew (Lucas and Peters, 2000). Meat toughness is predictable from the connective tissue content, and accounts for much of the variation in preference among Western consumers (Bender, 1982; Dransfield, 1994; Purslow, 1999). Cooking above 80 °C coagulates the connective tissue collagen and hydrolyzes it to a soluble protein (gelatin). This allows muscle fibers to be easily separated, and gives them a short, brittle texture allowing easy mastication (Birch et al., 1986). Cooked meat is therefore much easier to eat than raw meat.

We know of no data on how rapidly humans can ingest the raw meat of wild animals. For an estimate of the efficiency of eating raw meat, therefore, we turn to data from chimpanzees (*Pan troglodytes*). Chimpanzees are a potentially useful

model because like *Homo*, they show no signs of dental adaptation to chewing meat, and in relation to body weight their jaws and chewing teeth are approximately the same size as in humans (between *Homo ergaster* and *H. sapiens*, Wood, 1995). Chimpanzees might therefore be expected to chew meat at roughly similar rates to humans. Chimpanzees are also avid predators that eat various wild mammals (mostly monkeys and ungulates) up to approximately 10 kg, always raw and normally freshly killed. They prefer meat that is relatively tender, such as younger prey, and blood, feces, brains and guts (Goodall, 1986). (Tenderness is greater in younger animals, Shorthose and Harris, 1990.) Prey items are sometimes abandoned after the softer parts have been eaten (personal observation).

Chimpanzees tend to eat their meat very slowly. Unfortunately exact rates of chewing are difficult to observe in the wild, because prey items tend to be shared among consumers that scatter and hide. However, three well-observed cases that were apparently typical allow us to estimate intake rates. First, Goodall (1986) recorded a large infant baboon prey (*Papio anubis*) that was eaten for almost 9 h by a single adult male chimpanzee. After he had finished with it the head, arms, legs and part of the torso remained, and were then eaten by others. A large infant (weaned) baboon is estimated to weigh 3.8 kg (Lee, 1991). Second, a mother chimpanzee, her infant son and her late-adolescent daughter fed on a newborn bushbuck (*Tragelaphus scriptus*) for 4.8 h, at which point the legs (somewhat depleted) and backbone were still held together by skin (Goodall, 1986, p. 296). A new-born bushbuck probably weighs less than 4 kg, given that new-borns of nyala (*T. angasi*) weigh 5.60 kg and nyala females are 2–4 times the body weight of bushbuck (Lee, 1991; Nowak, 1999). Third, a juvenile red colobus monkey (*Colobus badius*) that was estimated to weigh 4 kg was chewed for a total of 11.5 ‘chimpanzee-hours’ by nine chimpanzees (Wrangham, 1975).

Based on these observations, we can estimate the rate of calorie intake for chimpanzees eating raw meat. Assuming that 20% of the prey remained in the case of the baboon and bushbuck, and scoring only adolescent or adult consumers, chimpanzees ate prey animals at a rate of 333–348 g/h, including skin and bones. From our measurements, red colobus meat contains approximately 3% fat, or approximately 115 cal/100 g.

This means that chimpanzees eating red colobus meat would have ingested approximately 382–400 cal/h. Since bone and skin, which have lower caloric value than meat, accounted for much of the carcass weight (perhaps 30–50%), actual caloric intake would be less than 400 cal/h. An upper bound for the rate of energy intake, therefore, is 400 cal/h.

The energy requirements for a *Homo erectus* female have been estimated at 2269–2487 per day (Aiello and Key, 2002). At 400 cal/h, a *Homo erectus* would therefore have had to chew raw meat for 5.7–6.2 h/day to satisfy her daily energy needs, i.e. 47–51% of a 12-h day. While similar to the total amount of time spent feeding by chimpanzees (46.9–55.7%, Wrangham, 1992), this time allocation clearly far exceeds any human value for time spent chewing per day. Note that it does not include the time taken to harvest and prepare the meat. Of course it is highly unlikely that *Homo erectus* would have survived on meat alone, since large quantities of animal protein unbuffered by fat or carbohydrates are physiologically detrimental (Milton, 1987). The important point, however, is that raw meat appears difficult for a hominoid to eat. Possibly, for instance, chimpanzee molars are poorly adapted for holding and slicing raw connective tissue. Equally, chimpanzee jaw muscles may be too weak to be effective (unlike baboons, which eat meat much faster than chimpanzees, Wrangham, 1975).

Accordingly, these calculations imply that for meat to have become an important part of the diet, one of three conclusions is necessary. First, pre-cooking humans might have spent much longer chewing their food than any contemporary populations do. Second, unrecognized differences in mastication efficiency between chimpanzees and pre-cooking humans might have allowed humans to chew meat more efficiently than chimpanzees do. Or third, humans must have had some system for tenderizing meat. The chimpanzee model suggests that the most likely solution is the third. We therefore suggest that an important technique that enabled humans to tenderize meat was cooking.

In sum, this discussion suggests that humans are poorly adapted to eating raw meat, and that the adoption of cooking would have facilitated the increased use of meat as a food source.

6. Discussion

6.1. Cooking and the digestive system

It might reasonably have been expected that the adoption of cooking would not have led to any changes in human digestion. After all, cooking makes food easier to eat, which means that no special adaptations are required to process cooked food. However, current evidence suggests that humans are capable of living on raw food only under unusual circumstances, such as a relatively sedentary lifestyle in a well-supported urban environment. Important theoretical obstacles to living on raw food in the wild include both the low digestibility of much raw plant food, and the toughness of much raw meat. Cooking has been practiced for enough time to allow evolutionary adaptation. These points suggest that humans are evolutionarily constrained to eating foods that are so digestible and easily chewed that cooking is normally obligatory. They suggest that after cooking was adopted, humans lost the ability to survive on raw food except under unusual circumstances (e.g. eating blubber), perhaps because some of the characteristics needed for eating raw food were unnecessarily costly. The implication is that although the adoption of cooked food imposed no new dietary restraints, it created opportunities for humans to adapt by using diets of high caloric density more efficiently. Selection for such efficiency, we propose, led to an inability to survive on raw-food diets in the wild.

Important questions therefore arise concerning what limits the human ability to utilize raw food. The principal effect of cooking considered to date has been a reduction in tooth size and jaw size over evolutionary time. Thus Brace et al. (1991) noted that human molar size started falling approximately 100 000 years ago, and suggested that this was a consequence of eating cooked food. Subsequent population variation in the extent and timing of dental reduction is broadly explicable by regional variation in the times when improvements in cooking technology were adopted (Brace, 1995). It is also possible that the earliest impact of cooking was the reduction of tooth and jaw size that accompanied the evolution of *Homo ergaster* approximately 1.9 million years ago (Wrangham et al., 1999). If so, the fall in tooth size and jaw size that starts around 100 000 years ago may

prove to result from later modifications in cooking technique, such as the adoption of boiling.

The evolution of soft parts of the digestive system is harder to reconstruct because they leave no fossil record. Human digestive anatomy differs from the other great apes in ways that have traditionally been explained as adapted to a high meat diet. Differences include the smaller gut volume, longer small intestine, smaller cecum and colon, and faster gut passage rate of humans (Chivers and Hladik, 1984; Martin et al., 1985; MacLarnon et al., 1986; Milton and Demment, 1988; Hladik et al., 1999). All such features are essentially adaptations to a diet of relatively high caloric density, however, and may therefore be at least as well explained by the adoption of cooking as by raw-meat-eating. Testing between the cooking and raw-meat model for understanding human digestive anatomy is therefore warranted.

The impact of cooking in drying, detoxifying and enriching foods suggests other areas in which to look for adaptations, including the production of salivary and gastric fluids, the response to chemicals generated by cooking, and the detoxification of chemicals destroyed by cooking. Understanding the effects of adaptation to a cooked diet may be important, for example, for predicting the physiological effects of drugs in humans compared to other primates. But little is currently known about differences in digestive physiology between humans and other apes (Milton, 1999). Further investigation is therefore needed of the ways in which human digestive physiology is constrained by the need for cooked food, especially plant foods.

6.2. *Cooking and human evolution*

Beyond the digestive system, various evolutionary influences of cooking are expected in the same way as other changes in food supply. Many aspects of species biology are adapted to the nature and distribution of their food supply (e.g. Lee, 1999). Cooking has particularly dramatic effects on the food supply, including softening food, increasing food availability, and forcing food distribution into predictable clumps around fires. Indeed, over evolutionary history the adoption of cooking should probably be regarded as one of the largest ever improvements in dietary quality, and one of the largest ever changes in food distribution and availability. Comparable changes include increased

meat-eating, agriculture and animal domestication, all of which have clearly had massive effects. An equivalent magnitude of species adaptations can be expected to have followed the adoption of cooking.

For example, cooking seems likely to have influenced life-history. Thus human weaning occurs 30–40% earlier than expected for a primate of our body mass (Low, 2000). No specific suggestions have been made until recently for how juvenile humans were able to find foods sufficiently soft for them to eat (Knott, 2001; Aiello and Key, 2002). We suggest that the adoption of cooking, by making raw foods soft enough for juveniles to chew, may have facilitated the early weaning and short inter-birth intervals that characterize the human life-history (Galdikas and Wood, 1980; Low, 2000). Recent variations in cooking technology are similarly associated with variation in the age of weaning (Bullington, 1991). Humans also have low intrinsic rates of mortality compared to other apes (Hill et al., 2001). If superior diets have enabled humans to maintain a more effective immune system, cooking may have contributed to the evolution of reduced mortality.

As a second example, cooking necessitates the collection of food into temporary piles. Food-piles are a novel form of food distribution in comparison with non-human primates, but in other species all such concentrated resources invariably generate competition. This implies that cooking would have generated new forms of social behavior adapted to regulating the new pressures of feeding competition. Possibly, for example, adult females (the smaller and socially subordinate sex) formed protective alliances with individual adult males, leading to a system of 'respect-for-possession' among males and contributing to the sexual division of labor (Wrangham et al., 1999). While such scenarios have yet to be explored in detail, the general point is that the adoption of cooking created a form of food distribution with novel implications for the regulation of social behavior. New forms of social behavior would be supported by modifications in psychological tendency. Like other major changes in dietary distribution, the adoption of cooking can therefore be expected to have had large ultimate effects on evolutionary psychology.

In sum, cooking appears to be a universal with sufficient evolutionary history to have affected human biology in various ways. It can be expected to have had major effects on digestive biology, as

well as other features of human biology affected by the quality, abundance and distribution of the diet.

Humans are sometimes claimed to be so inventive that it is meaningless to characterize our species as having experienced any particular environment of evolutionary adaptedness (Potts, 1998; Ehrlich and Feldman, 2003). But while cooking gave humans dietary flexibility, it also constrained our species into being creatures adapted to diets of high caloric density, prepared around temporary food-piles, and committed to the control of fire and the social relations that were therefore necessitated. Cooking may be cultural, but current evidence suggests that its effects have fed back into our biology, and have thereby created constraints that importantly shape and define our evolutionary biology. The nature of those constraints have barely begun to be explored.

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References

- Aiello, L.C., Key, C., 2002. Energetic consequences of being a *Homo erectus* female. *Am. J. Hum. Biol.* 14, 551–565.
- Aoki, K., 1991. Time required for gene frequency change in a deterministic model of gene culture coevolution, with special reference to the lactose absorption problem. *Theor. Popul. Biol.* 40, 354–368.
- Ayankunbi, M.A., Keshinro, O.O., Egele, P., 1991. Effect of methods of preparation on the nutrient composition of some cassava products—Garri (Eba), Lafun and Fufu. *Food Chem.* 41, 349–354.
- Barampama, Z., Simard, R.E., 1995. Effects of soaking, cooking and fermentation on composition, in-vitro digestibility and nutritive value of common beans. *Plant Foods Hum. Nutr.* 48, 349–365.
- Barr, S.I., 1999. Vegetarianism and menstrual cycle disturbances: is there an association? *Am. J. Clin. Nutr.* 70, 549S–554S.
- Bar-Yosef, O., 2001. From sedentary foragers to village hierarchies: the emergence of social institutions. *Proc. Br. Acad.* 110, 1–38.
- Bender, A.E., 1982. *Dictionary of Nutrition and Food Technology*. Butterworths, London.
- Birch, G.G., Cameron, A.G., Spencer, M., 1986. *Food Science*. Pergamon Press, Oxford.
- Blurton-Jones, N., Hawkes, K., O’Connell, J.F., 1999. Some current ideas about the evolution of the human life history. In: Lee, P.C. (Ed.), *Comparative Primate Socioecology*. Cambridge University Press, Cambridge, pp. 140–165.
- Boaz, N.T., Almquist, A.J., 1997. *Biological Anthropology: A Synthetic Approach to Human Evolution*. Prentice Hall, Upper Saddle River, New Jersey.
- Boyd, R., Silk, J.B., 2000. *How Humans Evolved*. W.W. Norton, New York.
- Brace, C.L., 1995. *The Stages of Human Evolution*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Brace, C.L., 1996. Modern human origins and the origins and the dynamics of regional continuity. In: Akazawa, T., Szathmáry, E.J.E. (Eds.), *Prehistoric Mongoloid Dispersals*. Oxford University Press, Oxford, pp. 81–112.
- Brace, C.L., 1999. An anthropological perspective on ‘race’ and intelligence: the non-clinical nature of human cognitive capabilities. *J. Anthropol. Res.* 55, 245–264.
- Brace, C.L., 2002. The raw and the cooked: a Plio/Pleistocene Just So Story, or sex, food, and the origin of the pair bond. *Soc. Sci. Inf.* 39, 17–27.
- Brace, C.L., Rosenberg, K.R., Hunt, K.D., 1987. Gradual change in human tooth size in the late Pleistocene and post-Pleistocene. *Evolution* 41, 705–720.
- Brace, C.L., Smith, S.L., Hunt, K.D., 1991. What big teeth you had Grandma! Human tooth size, past and present. In: Kelley, M.A., Larsen, C.S. (Eds.), *Advances in Dental Anthropology*. Wiley-Liss, New York, pp. 33–57.
- Brain, C.K., 1993. The occurrence of burnt bones at Swartkrans and their implications for the control of fire by early hominids. In: Brain, C.K. (Ed.), *Swartkrans. A Cave’s Chronicle of Early Man*. Transvaal Museum Monograph No. 8, Transvaal, pp. 229–242.
- Bravo, L., 1999. Effect of processing on the non-starch polysaccharides and in vitro starch digestibility of legumes. *Food Sci. Technol. Int.* 5, 415–423.
- Bravo, L., Siddhuraju, P., Saura-Calixto, F., 1998. Effect of various processing methods on the in vitro starch digestibility and resistant starch content of Indian pulses. *J. Agric. Food Chem.* 46, 4667–4674.
- Brooks, A.S., 1996. Behavior and human evolution. In: Meikle, W.E., Howell, F.C., Jablonski, N.G. (Eds.), *Contemporary Issues in Human Evolution*. California Academy of Sciences, San Francisco, CA, pp. 135–166.
- Bullington, J., 1991. Deciduous dental microwear of prehistoric juveniles from the Lower Illinois River Valley. *Am. J. Phys. Anthropol.* 84, 59–74.
- Butrum, R.R., Clifford, C.K., Lanza, E., 1988. NCI dietary guidelines: rationale. *Am. J. Clin. Nutr.* 48, 888–895.
- Cavalli-Sforza, L.L., Menozzi, P., Piazza, A., 1994. *The History and Geography of Human Genes*. Princeton University Press, Princeton.
- Chitra, U., Singh, U., Rao, P.V., 1996. Phytic acid, in vitro protein digestibility, dietary fiber, and minerals of pulses as influenced by processing methods. *Plant Foods Hum. Nutr.* 49, 307–316.
- Chivers, D.J., Hladik, C.M., 1984. Diet and gut morphology in primates. In: Chivers, D.J., Wood, B.A., Bilsborough, A. (Eds.), *Food Acquisition and Processing in Primates*. Plenum Press, New York, pp. 213–230.
- Conklin-Brittain, N., Wrangham, R.W., Smith, C.C., 2002. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar, P., Teaford, M.

- (Eds.), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport, Connecticut, pp. 61–76.
- Coon, C.S., 1954. *The Story of Man: From the First Human to Primitive Culture and Beyond*. Knopf, New York.
- Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H.A., Speth, J.D., 2000. Plant–animal subsistence ratios and macronutrient energy estimations in worldwide hunter–gatherer diets. *Am. J. Clin. Nutr.* 71, 682–692.
- Dransfield, E., 1994. Tenderness of meat, poultry and fish. In: Pearson, A.M., Dutson, T.R. (Eds.), *Quality Attributes and Their Measurements in Meat, Poultry and Fish Products*. Blackie Academic and Professional, London, pp. 289–315.
- Draper, H.H., 1977. The aboriginal Eskimo diet in modern perspective. *Am. Anthropol.* 79, 309–316.
- Durham, W.H., 1991. *Coevolution: Genes, Culture, and Human Diversity*. Stanford University Press, Stanford CA.
- Eaton, S.B., Konner, M., 1985. Paleolithic nutrition: a consideration of its nature and current implications. *N. Engl. J. Med.* 312, 283–289.
- Ehrlich, P., Feldman, M.W., 2003. Genes and cultures: what creates our behavioral phoneme? *Curr. Anthropol.* 44, 87–107.
- Fuel, 2.3 Nutrition Software, 2000. Logiform International Inc. and the Coaching Association of Canada.
- Galdikas, B., Wood, J., 1980. Birth spacing patterns in humans and apes. *Am. J. Phys. Anthropol.* 63, 185–191.
- Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Harvard University Press, Cambridge MA.
- Gott, B., 2002. Fire-making in Tasmania: absence of evidence is not evidence of absence. *Curr. Anthropol.* 43, 649–656.
- Goudsblom, J., 1992. *Fire and Civilization*. Penguin, New York.
- Gould, S.J., 2002. *The Structure of Evolutionary Theory*. Harvard University Press, Cambridge MA.
- Harris, D., 1992. Human diet and subsistence. In: Jones, S., Martin, R., Pilbeam, D. (Eds.), *The Cambridge Encyclopedia of Human Evolution*. Cambridge University Press, Cambridge, pp. 69–74.
- Harris, M., Ross, E.B., 1987. *Food and Evolution: Toward a Theory of Human Food Habits*. Temple University Press, Philadelphia PA.
- Hatley, T., Kappelman, J., 1980. Bears, pigs, and plio-pleistocene hominids: a case for the exploitation of belowground food resources. *Hum. Ecol.* 8, 371–387.
- Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., Wrangham, R.W., 2001. Mortality rates among wild chimpanzees. *J. Hum. Evol.* 40, 437–450.
- Hladik, C.M., Chivers, D.J., Pasquet, P., 1999. On diet and gut size in non-human primates and humans: is there a relationship to brain size? *Curr. Anthropol.* 40, 695–697.
- Holm, J., Lundquist, I., Björck, I., Eliasson, A.C., Asp, N.G., 1988. Degree of starch gelatinization, digestion rate of starch in vitro, and metabolic response in rats. *Am. J. Clin. Nutr.* 47, 1010–1016.
- James, S.R., 1989. Hominid use of fire in the Lower and Middle Pleistocene: a review of the evidence. *Curr. Anthropol.* 30, 1–26.
- Jurmain, R., Nelson, H., 1994. *Introduction to Physical Anthropology*. West Publishing Company, St. Paul, Minnesota.
- Kataria, A., Chauhan, B.M., 1988. Contents and digestibility of carbohydrates of mung beans (*Vigna radiata* L.) as affected by domestic processing and cooking. *Plant Foods Hum. Nutr.* 38, 51–59.
- Kelly, R.L., 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Smithsonian Institution, Washington, D.C.
- Khalil, M.M., 2001. Effect of soaking, germination, autoclaving and cooking on chemical and biological value of guar compared with faba bean. *Nahrung* 45, 246–250.
- Kingman, S., Englyst, H., 1994. The influence of food preparation methods on the in vitro digestibility of starch in potatoes. *Food Chem.* 49, 181–186.
- Knott, C., 2001. Female reproductive ecology of the apes: implications for human evolution. In: Ellison, P. (Ed.), *Reproductive Ecology and Human Evolution*. Aldine, New York, pp. 429–463.
- Koebnick, C., Strassner, C., Hoffmann, I., Leitzmann, C., 1999. Consequences of a longterm raw food diet on body weight and menstruation: results of a questionnaire survey. *Ann. Nutr. Metab.* 43, 69–79.
- Kretzoi, M., Dobosi, V.T. (Eds.), 1990. *Vértesszölös: Site, Man and Culture*. Akadémiai Kiadó, Budapest.
- Laden, G., Wrangham, R.W., 2003. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and the origin of the Australopithecines. *J. Hum. Evol.*, in press.
- Lee, P.C., 1991. Growth, weaning and maternal investment from a comparative perspective. *J. Zool. (Lond.)* 225, 99–114.
- Lee, P.C. (Ed.), 1999. *Comparative Primate Socioecology*. Cambridge University Press, Cambridge.
- Leonard, W.R., Robertson, M.L., 1997. Comparative primate energetics and hominid evolution. *Am. J. Phys. Anthropol.* 102, 265–281.
- Lewin, R., 1993. *Human Evolution: An Illustrated Introduction*. Blackwell, Oxford.
- Low, B., 2000. *Why Sex Matters*. Princeton University Press, Princeton NJ.
- Lucas, P.W., Peters, C.R., 2000. Function of postcanine tooth shape in mammals. In: Teaford, M., Smith, M.M., Ferguson, M.W.J. (Eds.), *Development, Function, and Evolution of Teeth*. Cambridge University Press, Cambridge, pp. 282–289.
- MacLarnon, A.M., Martin, R.D., Chivers, D.J., Hladik, C.M., 1986. Some aspects of gastro-intestinal allometry in primates and other mammals. In: Sakka, M. (Ed.), *Definition et Origines de L'Homme*. Editions du CNRS, Paris, pp. 293–302.
- Mann, N., 2000. Dietary lean red meat and human evolution. *Eur. J. Nutri.* 39, 71–79.
- Marconi, E., Ruggeri, S., Cappelloni, M., Leonardi, D., Carnovale, E., 2000. Physicochemical, nutritional, and microstructural characteristics of chickpea (*Cicer arietinum* L.) and common beans (*Phaseolus vulgaris* L.) following microwave cooking. *J. Agric. Food Chem.* 48, 5986–5994.
- Martin, R.D., Chivers, D.J., MacLarnon, A.M., Hladik, C.M., 1985. Gastrointestinal allometry in primates and other mammals. In: Jungers, W.L. (Ed.), *Size and Scaling in Primate Biology*. Plenum, New York, pp. 61–89.
- Milton, K., 1987. Primate diets and gut morphology: implications for hominid evolution. In: Harris, M., Ross, E.B. (Eds.), *Food and Evolution: Towards a Theory of Human*

- Food Habits. Temple University Press, Philadelphia, PA, pp. 93–115.
- Milton, K., 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol.* 8, 11–21.
- Milton, K., 2000. Back to basics: why foods of wild primates have relevance for modern human health. *Nutrition* 16, 480–483.
- Milton, K., 2002. Hunter–gatherer diets: wild foods signal relief from diseases of affluence. In: Ungar, P.S., Teaford, M.F. (Eds.), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport, CT, pp. 111–122.
- Milton, K., Demment, M.W., 1988. Chimpanzees fed high and low fiber diets and comparison with human data. *J. Nutr.* 118, 1082–1088.
- Muir, J.G., O’Dea, K., 1992. Measurement of resistant starch: factors affecting the amount of starch escaping digestion in vitro. *Am. J. Clin. Nutr.* 56, 123–127.
- Nowak, R.M., 1999. *Walker’s Mammals of the World*. Johns Hopkins University Press, Baltimore MD.
- O’Connell, J.F., Hawkes, K., Blurton-Jones, N.G., 1999. Grandmothering and the evolution of *Homo erectus*. *J. Hum. Evol.* 36, 461–485.
- O’Connell, J.F., Hawkes, K., Lupo, K.D., Blurton-Jones, N.G., 2002. Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.* 43, 831–872.
- O’Dea, K., 1991. Traditional diet and food preferences of Australian Aboriginal hunter–gatherers. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 334, 223–241.
- Ortner, D.S. (Ed.), 1983. *How Humans Adapt: A BioCultural Odyssey*. Smithsonian Institution Press, Washington D.C.
- Park, M.A., 1996. *Biological Anthropology*. Mayfield, Mountain View, CA.
- Periago, M.J., Englyst, H.N., Hudson, G.L., 1996. The influence of thermal processing on the non-starch polysaccharide (NSP) content and in vitro digestibility of starch in peas (*Pisum sativum*, L). *Food Sci. Technol.-Leb.* 29, 33–40.
- Periago, M.J., Ros, G., Casas, J.L., 1997. Non-starch polysaccharides and in vitro starch digestibility of raw and cooked chick peas. *J. Food Sci.* 62, 93–96.
- Phillips, K.M., Palmer, J.K., 1991. Effect of freeze-drying and heating during analysis on dietary fiber in cooked and raw carrots. *J. Agric. Food Chem.* 39, 1216–1221.
- Potts, R., 1998. Environmental hypotheses of hominin evolution. *Yb. Phys. Anthropol.* 41, 93–138.
- Purslow, P.P., 1999. The Intramuscular Connective Tissue Matrix and Cell/Matrix Interactions in Relation to Meat Toughness. 46th International Congress of Meat Science and Technology, Yokohama, Japan, 9, pp. 210–219.
- Ragir, S., 2000. Diet and food preparation: rethinking early hominid behavior. *Evol. Anthropol.*, 153–155.
- Rao, P.U., 1996. Nutrient composition and biological evaluation of mesta (*Hibiscus sabdariffa*) seeds. *Plant Foods Hum. Nutr.* 49, 27–34.
- Relethford, J.H., 1997. *The Human Species: An Introduction to Biological Anthropology*. Mayfield, Mountain View, CA.
- Rowlett, R.M., 2000. Fire control by *Homo erectus* in East Africa and Asia. *Acta Anthropol. Sin.* 19, 198–208.
- Ruales, J., Nair, B.M., 1994. Properties of starch and dietary fiber in raw and processed quinoa (*Chenopodium quinoa*, Willd) seeds. *Plant Foods Hum. Nutr.* 45, 223–246.
- Sagum, R., Arcot, J., 2000. Effect of domestic processing methods on the starch, non-starch polysaccharides and in vitro starch and protein digestibility of three varieties of rice with varying levels of amylose. *Food Chem.* 70, 107–111.
- Scrimshaw, N.S., 1983. Food: past, present, and future. In: Ortner, D.S. (Ed.), *How Humans Adapt: A Biocultural Odyssey*. Smithsonian Institution Press, Washington, D.C., pp. 227–253.
- Shorthose, W.R., Harris, P.V., 1990. Effect of animal age on the tenderness of selected beef muscles. *J. Food Sci.* 55, 1–14.
- Slavin, J.L., Jacobs, D., Marquart, L., 2001. Grain processing and nutrition. *Crit. Rev. Food Sci. Nutr.* 40, 309–326.
- Smith, C.S., Martin, W., Johansen, K.A., 2001. Sego lilies and prehistoric foragers: return rates, pit ovens, and carbohydrates. *J. Archaeol. Sci.* 28, 169–183.
- Smith, E.A., 1991. *Inujjamiut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy*. Aldine, Hawthorne, NY.
- Speth, J.D., Tchernov, E., 2001. Neandertal hunting and meat-processing in the Near East: evidence from Kebara Cave (Israel). In: Stanford, C.T., Bunn, H.T. (Eds.), *Meat-eating and Human Evolution*. Oxford University Press, Oxford, pp. 52–72.
- Stahl, A.B., 1984. Hominid diet before fire. *Curr. Anthropol.* 25, 151–168.
- Stanford, C.T., Bunn, H.T., 2001. *Meat-eating and Human Evolution*. Oxford University Press, Oxford.
- Stefansson, V., 1913. *My Life with the Eskimo*. MacMillan, New York.
- Stefansson, V., 1960. *Cancer: Disease of Civilization?*. Hill and Wang, New York.
- Straus, L.G., 1989. On early hominid use of fire. *Curr. Anthropol.* 30, 488–491.
- Teaford, M.F., Ungar, P.S., Grine, F.E., 2002. Paleontological evidence for the diets of African Plio-Pleistocene hominins with special reference to early *Homo*. In: Ungar, P.S., Teaford, M.F. (Eds.), *Human Diet: Its Origin and Evolution*. Bergin & Garvey, Westport, CT, pp. 143–166.
- Trout, D.L., Behall, K.M., Osilesi, O., 1993. Prediction of glycemic index for starchy foods. *Am. J. Clin. Nutr.* 58, 873–878.
- Ungar, P.S., Teaford, M.F. (Eds.), 2002. *Human Diet: Its Origin and Evolution*. Bergin and Garvey, Westport, CT.
- Urooj, A., Puttaraj, S., 1994. Effect of processing on starch digestibility in some legumes—an in vitro study. *Nahrung* 38, 38–46.
- Veena, A., Urooj, A., Puttaraj, S., 1995. Effect of processing on the composition of dietary fiber and starch in some legumes. *Nahrung* 39, 132–138.
- Wood, B.A., 1995. Evolution of the early hominin masticatory system: mechanisms, events, and triggers. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 438–448.
- Wrangham, R.W., 1975. *The Behavioral Ecology of Chimpanzees in Gombe National Park, Tanzania* [PhD], Cambridge University.

- Wrangham, R.W., 1992. Living naturally: aspects of wild environments relevant to captive chimpanzee management. In: Erwin, J. (Ed.), *Chimpanzee Conservation and Public Health: Environments for the Future*. Diagon, Rockville, MD, pp. 71–81.
- Wrangham, R.W., 2001. Out of the pan, into the fire: from ape to human. In: de Waal, F.B.M. (Ed.), *Tree of Origin*. Harvard University Press, Cambridge, MA, pp. 119–143.
- Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N.L., 1999. The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthrop.* 40, 567–594.
- Yiu, S.H., 1993. Food microscopy and the nutritional quality of cereal foods. *Food Struct.* 12, 123–133.
- Zootrition, 2.0 Software, 2002. Wildlife Conservation Society, New York.