Tropical forager gastrophagy and its implications for extinct hominin diets.

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Abstract
Reconstruction of extinct hominin diets is currently a topic of much interest and debate, facilitated by new methods such as the analysis of dental calculus. It has been proposed, based on chemical analyses of calculus, that Neanderthals self-medicated, yet this conclusion has been questioned. Gastrophagy has been suggested as an alternative explanation for the Neanderthal data, based on ethnographic analogies, which show this practice to have been widespread in traditional extant *Homo sapiens* diets, and nutritional evidence for its benefits at high latitudes. Here we expand the discussion of the potential importance of gastrophagy in human evolution by considering its role for an extant group of tropical foragers, the Hadza of Tanzania, and questioning its role in the diets of extinct tropical hominin species. Gastrophagy is frequently practiced among the Hadza and adult men in particular consume substantial, seasonally variable, amounts of prey guts. In addition to the important fact that gastrophagy is not a rare event, this demographic information may be useful in interpreting evidence from archaeological samples. The consumption of semi-digested chyme would have allowed extinct hominins to gain calories from plant sources without the cost of digesting them, possibly contributing to the encephalisation and shrinking of the gut in genus *Homo*. As an easy to process food-source, chyme could have likewise been an important food source for the old and the young, potentially playing a part in reducing inter-birth intervals and increasing reproductive success in our lineage. Thus gastrophagy may have played a key part in human evolution and its potentially confounding signal should be considered in future dietary reconstructions.

Introduction
The reconstruction of extinct hominin diets is currently a topic of much interest and debate, partly due to the novel use, in archaeological and anthropological disciplines, of methods such as dental calculus analysis (e.g., Henry et al., 2011; 2012; 2014, Hardy et al., 2012, Power et al.,

2014; 2015) and the study of faecal biomarkers (Sistiaga et al., 2014). As they sample the input and products of the body directly, both methods reduce the risk inherent in analysing dietary proxies, such as archaeological assemblages of bone, tool residue or use-wear, that the sample is not from food (e.g., Hardy, 2001, Buck & Stringer, 2014). Both methods also sample products not previously targeted in such analyses before, allowing for the possibility of new data from previously collected specimens/sediment. Most importantly for the purposes of this paper, however, these methods enable the study of vegetable components of fossil hominins' diets in much greater detail than pre-existing methods, such as isotope analysis.

The results of these new methods are not without their own ambiguities, however, and one article in particular has proved controversial: Hardy et al. (2012) analysed the dental calculus of five Neanderthals from El Sidrón cave, Spain. They found evidence compatible with the consumption of starchy foods, probably including grass seeds, cooking and, in one individual, the consumption of yarrow and camomile. Hardy and colleagues (2012; 2013) have asserted that the evidence for these forbs demonstrates Neanderthal self-medication. Their case rests on the low nutritional value of these plants, their bitter taste, and long-standing medical uses for both species amongst recent *Homo sapiens*. It is known from aDNA analysis (Lalueza-Fox et al., 2011) that at least one of the Neanderthals from this site (not one in Hardy and colleagues' sample) could taste bitter flavours, although it seems that there is variation in this trait for Neanderthals, as there is for *H. sapiens*, and indeed for chimpanzees (Perry et al., 2015). Hardy et al. (2012) contend that bitter plants are usually avoided as food, as their flavour may be evidence of toxicity. As Hardy and co-workers have pointed out (Huffman, 2003, Hardy et al., 2012; 2013), many animals self-medicate and it seems eminently plausible that Neanderthals, with their complex cognition and behaviour, would have done the same.

Self-medication is not the only possible scenario, however. A bitter flavour does not preclude a plant from being considered food. Many bitter foods are enjoyed by humans today, including both yarrow and camomile (Mabey, 1973, Kuhnlein & Turner, 1991, Nozedar, 2012). Furthermore, Krief et al. (2015) have recently shown that chimpanzees preferentially consume bitter leaves to augment the flavour of certain foods. If chimpanzees have complex conceptions of flavour, there seems no reason to believe Neanderthals would not also have such conceptions. As has previously been pointed out (Buck & Stringer, 2014), calculus analysis also suffers from the potential complication that not everything put into the mouth is food and it seems that Neanderthals made particularly intense use of their mouths as tools (e.g., Hylander, 1975, Smith, 1976, Krueger et al., 2012). In addition to these notes of caution for the interpretation of Neanderthal self-medication, two of us have suggested that another nonmedical explanation for yarrow and chemical compounds in the El Sidrón calculus could be gastrophagy, i.e., the consumption of the stomach and intestines, sometimes including the chyme (Buck & Stringer, 2014).

In our previous paper (Buck & Stringer, 2014), we showed that gastrophagy is a common part of traditional diets for recent *H. sapiens* from different ecological niches and with different subsistence strategies. Ethnographies report the consumption of stomachs or stomach contents of many different animals, from ostrich (Low, 2009) to buffalo (Lame Deer & Erdoes, 1972) to

walrus (Feduik, 2000) and varied reasons for consumption, including ritual (Peterson and Walhof, 2002), nutrition (Feduik, 2000, Andersen, 2005; see Buck & Stringer, 2014 for a discussion) and taste (Lame Deer & Erdoes, 1972, Feduik, 2000). In general these accounts garnered from the literature mention gastrophagy in passing, as it is seldom considered of much interest and is never the focus of the work. Older ethnographies also suffer from a Western bias that leads to the reporting of gastrophagy in terms of gleefully highlighting what was considered to be a disgusting habit of a primitive people, with the aim of entertaining, rather than considering the utility and importance of the practice (e.g., Kumlien, 1880).

The one group where gastrophagy has been more seriously analysed is that where its practice is most famous, amongst the Inuit. Two recent studies (Feduik, 2000, Andersen, 2005) in particular have considered the role that gastrophagy plays within wider Inuit diet and culture. In high latitude environments, where there is little edible vegetable food for humans, Inuit people consume the guts and chyme of a wide range of species, including ringed seal, bearded seal, narwhal, walrus, Arctic hare and reindeer (Feduik, 2000). Reindeer chyme, for example, is a good source of some of the vitamins and minerals important for human physiological maintenance; it is high in vitamin C, E and the precursor to vitamin A, Manganese, Calcium and Iron (Feduik, 2000, Andersen, 2005). It is also an important source of carbohydrates (Andersen, 2005), which are vital to avoid protein poisoning (Speth et al., 1991; Cordain et al., 2000).

The perils of extrapolating from extant (and technologically and culturally very complex) foragers to extinct hominins notwithstanding, there are obvious parallels to be drawn between the role that gastrophagy plays in the Inuit diet and its potential utility to Neanderthals living in commensurately vegetable-poor environments. These are not the only temperate-boreal hominins for which such a practice could have been beneficial, however. There is archaeological (Parfitt et al., 2010) and footprint (Ashton et al., 2014) evidence for hominins in Britain at Happisburgh in Norfolk at approximately 950-800 ka. Associated pollen, plant macro remains and insects suggest an environment that was distinctly cooler, or more continental, than Britain today, with much colder winters (Parfitt et al., 2010). It is not known which hominin species left the traces at Happisburgh, but currently the best candidate is *Homo antecessor* (Ashton et al., 2014), as described from remains at Gran Dolina, Spain at approximately 800-950 ka (Falguères, 2003, Berger et al., 2008). Since, based on current evidence, *H. antecessor* was less technologically sophisticated than *H. neanderthalensis*, how this species survived the British climate at this period is an interesting question. Physiological adaptation (such as increased body hair or genetic changes) is a possibility, but seasonal migration on the scale necessary to effect a real difference in winter climate seems unlikely, given the distance south that would be required. Behavioural adaptations to the cold such as dietary changes, therefore, are plausible as part of a composite strategy. Preferential gastrophagy is not cognitively demanding, and indeed is practiced by chimpanzees (Krief et al., 2015). As part of increased carnivory, as would be expected in higher latitudes (Cordain et al., 2000, Kelly, 2013), it could have been an important part of a novel cold-adapted niche, providing vital carbohydrates, vitamins and minerals for this species as well as for the much later Neanderthals.

Warm-adapted gastrophagy?

There is a strong case for the consumption of guts and chyme in temperate-boreal adapted hominins and we know from ethnographic accounts that it has also been practiced by extant warm-adapted forager groups such as aboriginal Australians, the Kuria of Tanzania, and the Khoesan and G/wi of the Kalahari (Silberbauer, 1981, O'Dea et al., 1991, Peterson & Walhof, 2002, Low, 2009). Silberbauer writing of the G/wi, for example, describes the consumption of prey guts and their contents:

> "The intestine is cleaned out below the duodenum which, with the small intestine, is roasted and eaten if there are a number of mouths to feed…The stomach of a large antelope is removed and placed on a bed of branches to keep it away from the sand; even in the driest season it holds 90-160 liters of liquor which, although not very pleasant-tasting, is a welcome substitute for water…The significance of rumen liquor from large antelopes is considerable in the waterless months (late March-late December)…Almost all [the liquor] was consumed by hunters and their helpers (rumen liquor is not normally carried back to camp with the edible portions)." (Silberbauer, 1981:477).

Many such accounts, however, lack detail of the circumstances of and reasons for gastrophagy. It is the aim of this paper, therefore, to examine the extent and context of gastrophagy within one particular warm-adapted forager group, the Hadza of Tanzania. The importance and context of gastrophagy in warm climates has been little considered and it is of utmost interest to palaeodietary reconstructions given that, for the vast majority of time, hominins have been exclusively tropical. Gastrophagy, in this case the consumption of the guts excluding the chyme, is practiced among the Hadza, as previously reported by Leach (2013). Here we firstly describe this practice in greater detail within the context of the well-studied Hadza diet and secondly consider the potential advantages of gastrophagy (including the consumption of chyme, as in the warm-adapted foragers listed above) to extinct warm-adapted hominins and the potential implications of gastrophagy for palaeodietary reconstructions.

The Hadza are a population of approximately 1000 individuals living in Northern Tanzania, with approximately 350 subsisting as full-time foragers; they are some of the last people in the world to do so. From the Hadza we hope to begin to answer questions about the quantity and frequency of gastrophagy, the identity of those who practice it within a group, the circumstances in which it is practiced, and which species are involved. From this information, it will then be possible to address questions such as whether gastrophagy would be sufficient to leave a trace in the calculus (or to affect other methods of dietary analysis), whether different age/sex groups might be expected to show differential evidence of gastrophagy, whether this a preferred or a fall-back food, if there seasonal differences, and which species of plant and animal should be considered in investigations of gastrophagy.

Hadza diet
The best long-running estimate of the plant to animal ratio (by kilocalories) eaten in camp is 53% plant-based, 32% animal-based, and 15% honey-based (Marlowe et al., 2014). Thus, as would be expected from foragers at this latitude (Cordain et al., 2000), the majority of the Hadza diet is vegetable, but there is still considerable animal input. The Hadza have sometimes been characterised as large game specialists (Bunn & Gurtov, 2014, Hawkes et al., 1991; 2001). However, Wood and Marlowe (2013) have demonstrated that across seven different camps,

79% of the animals that men brought back to camp weighed less than 10 kg. Observations of men while foraging also demonstrate that the Hadza are not targeting large game to the exclusion of small game and other foods (Wood et al., 2014a; Wood et al., 2014b). The Hadza consume the stomach and intestines of all the prey they kill. However, owing to Hadza butchery practices, detailed information about the weight of carcass elements is currently only available for large prey. The description of gastrophagy that follows, therefore, concerns only the large game fraction of their diet. In a sample of seven camps reported in Wood et al., (2013), 46 large game were killed over a period of 242 observation days, providing 1.9 kg of carcass flesh per person per day of observation.

A good general description of Hadza subsistence is available in Marlowe (2010). The greatest division in Hadza diet is sex-based, with women gathering and men hunting. Hadza men generally hunt alone, killing birds and mammals with bows and arrows, using poison in the case of larger game. By Kilocalories, meat forms about 40% of what men acquire, compared to just over 1% for women (Berbesque et al., 2011). Over the last two decades or so, the most frequently killed large game species (those heavier than ~ 32 kg) have been impala, greater kudu, lesser kudu, and zebra. Occasionally Hadza men also kill buffalo, eland, and giraffe. An aspect of forager diet largely over-looked until recently is food consumed away from camp, during daily foraging. Berbesque et al. (in review) have begun to address this important dietary component with a study of Hadza hunters' out of camp consumption over twelve years of observation across all seasons and all regions of Hadzaland. They found that, although there is a large degree of variation, a substantial amount, if not the majority of men's daily energy in-take, comes from foods consumed on walkabout (Berbesque et al., in review). Of relevance to discussions of gastrophagy, is that 59% percent of meat was eaten out of camp, though this varied with the size of the animal; 66% of small game was consumed out of camp compared to 31% of large game (Berbesque et al., in review).

For a variety of reasons, Hadza men consume more meat than women. Only initiated, i.e. fully adult, men are permitted to eat certain sacred parts of large animals (Woodburn, 1979). The specific carcass elements that are considered sacred varies somewhat by species, but they usually include the reproductive organs, the lungs, the heart, kidneys, kidney fat, spleen, pancreas, the trachea, the oesophagus, the tongue, and the abdominal fat. Initiated men eat these parts in seclusion, outside of the camp, away from females and uninitiated younger men and children. To view the consumption of these parts if one is not initiated is a very serious offense in Hadza culture. Men and women also report different food preferences, with meat more highly regarded by men, and more meat consumed in camp by men (Berbesque & Marlowe, 2009; Berbesque et al., 2011). Recently, sex differences in the Hadza diet have also been documented in research on the gut microbiome (Schnorr, 2014). These studies contribute to the understanding that males are eating a diet higher in animal protein. Sex differences in foraging patterns and return rates have even been documented in Hadza children (Crittenden et al., 2013), something rarely discussed as a potential factor when reconstructing ancestral human diets.

In addition to these contrasts between the sexes, there are seasonal differences in Hadza diet. Hunting is most successful during the late dry season (September-November), when water sources are restricted, allowing men to reliably predict where animals will travel to drink from remaining waterholes. Vegetable foods vary less throughout the year. Since the Hadza take such a large variety of species and range widely, they acquire a substantial amount of fruit and tubers across the year (Marlowe & Berbesque, 2009).

Hadza gastrophagy
Having shot and wounded an animal, Hadza men typically spend about 20 minutes following its tracks and blood spots in order to assess blood loss and direction of travel. Men may continue following the animal alone until it is found seriously wounded or dead. In other cases, hunters return to their residential group to enlist the help of a group of men to collectively track the wounded animal, if they find the dead animal they will then butcher the carcass as a team. During butchering, the hunters remove the stomach and intestines and set them aside. The stomach is sliced open and the partially digested plant materials inside are ejected by turning the stomach 'inside out'. Partially digested/fermented stomach contents remain adhering to the inside of the stomach. Faecal material from inside the intestines is similarly squeezed out by hand, unavoidably leaving some contents behind. Some parts of the kill are eaten (sometimes cooked) on the spot by hunters and others of tracking party. Men will often slice off small portions of the stomach and consume it raw (Figure 1) and liver is also eaten raw early in the butchery process. Among the first parts of the animals to be cooked and eaten at the kill site are the intestines as they are very thin, and thus can be roasted and eaten quickly. The remaining carcass after preliminary consumption is typically brought back to camp, to be roasted and boiled and eaten by other members of the group.

Figure 1: A Hadza hunter consuming raw stomach at the site of his impala kill.

Researchers and field assistants weigh carcass elements brought to camp by Hadza hunters, usually recording the weights of carcass elements as they are grouped and presented by the hunters. In most cases, the stomach or intestines are not weighed and recorded individually, but as part of a group of elements labelled 'organs' or 'intestines and stomach'. In the case of small game, which are usually not butchered before being brought to camp, the only weight recorded is that of the whole carcass. However, in nine cases, derived from work in a camp in August and September 2005 (Table 1) we can show that a considerable weights of large game gut (particularly from larger species, such as buffalo, see Figure 2) were regularly brought back and consumed by the camp. The stomachs of all prey are eaten, but based on body weight and frequency of capture, the species likely to contribute most to Hadza gastrophagy are impala, dik-dik, eland, zebra, kudu and buffalo.

These data do not account for any guts consumed by the hunters at the kill site, although a significant portion of meat is consumed at this time, particularly in the case of small game

(Berbesque et al., in review). Van Zyl & Ferreira (2004) have estimated that for an average adult impala the emptied guts (oesophagus, rumen, reticulum, omasum, abomasum, small intestine, large intestine, and caecum) weigh about 5.7 kg (stomach = 4.8 kg, intestines = 0.9 kg). Accepting that there are likely to be differences with region and season and that there is no information on the maturity of the impala in the Hadza data, this allows us to make very rough calculations of what proportion of impala guts are likely to have been eaten at kill sites. Where combined weights are known, the impala guts recorded by BMW (Table 1) range from 1.9-4.3 kg (mean = 3.3 kg, n = 5) and the stomachs range from 1-1.9 kg (mean = 1.4 kg, n = 8). This means that around 2.4 kg of guts (around 40%), or 3.4 kg of stomach (around 70%) are being eaten before the carcasses' return to camp. These estimations will, of course, need to be verified with more data from the field, but they likely show a marked difference in gastrophagy between men (hunters) and women and thus echo Silberbauer's (1981, see above) findings from the G/wi, that much gastrophagy is practiced out of camp.

Table 1: Preliminary data showing guts brought back to camp by Hadza hunters from 8 camps over 2 months in 2005 (BMW). * Either not brought back to camp, or weighed with other parts listed as "organs". ** Not brought back to camp.

Date	Carcass Number	Species	Part	Weight of part when brought to camp (kg)	Combined weight of guts (kg)
14-Aug-05	18	Impala	Stomach	1.9	
			Intestines	1.8	3.7
22-Aug-05	243	Impala	Stomach	1.5	
			Intestines	2	3.5
23-Aug-05	335	Impala	Stomach	1	
			Intestines	Unknown*	
26-Aug-05	391	Impala	Stomach	1.6	
			Intestines	1.6	3.2
26-Aug-05	401	Impala	Stomach	1.8	
			Intestines	Unknown*	
1-Sep-05	526	Impala	Stomach	1	
			Intestines	Unknown*	
1-Sep-05	536	Impala	Stomach	1	
			Intestines	0.9	1.9
1-Sep-05	545	Impala	Stomach	1.5	
			Intestines	2.8	4.3
2-Sep-05	580	Buffalo	Stomach	14 kg	
			Intestines	Unknown**	

Figure 2. A Hadza woman carrying the ribs and stomach of a buffalo from a kill site to her house.

The contribution of gastrophagy to Hadza diet

Whilst more information is needed, we can start to address some of the key questions identified above regarding the role of gastrophagy in the Hadza. Larger samples, information on small game as well as large game and data on the amount of guts eaten at kill sites, are needed to confidently quantify the contribution of gastrophagy to the Hadza diet, but frequent and considerable amounts (depending on size of kill) of guts are clearly eaten. This is not a rare occurrence, nor a fall-back food, but a normal part of day-to-day diet. Although guts are eaten by the entire group, the fact that gastrophagy is practiced at kill sites means that it is a much more important part of male diets than female diets. Given that males also consume more meat in camp than females (Berbesque et al., 2011), they are additionally likely to consume a higher proportion of the guts in camp. As detailed above, the guts of all hunted species are eaten but impala, dik-dik, eland, zebra, kudu and buffalo contribute most meat (and so, guts) to the Hadza diet. Hunting is easier in the dry season, when animals can be found more predictably, meaning that gastrophagy will be greater in these months. From this information, we might expect that evidence of gastrophagy could be present in Hadza dental calculus, as

suggested for the Neanderthals of El Sidrón (Buck & Stringer, 2014). Plant microfossils of interest would be those from plants eaten by the grazing species identified above, particularly those from plants which are not also eaten first-hand by the Hadza, such as grasses and herbaceous vegetation. The likelihood of finding such evidence would be highest in adult (male) hunters, as this class of individual would have engaged in the highest levels of gastrophagy. This information urges caution in palaeodietary studies (e.g., calculus studies) which may sample only one sex.

The reasons for Hadza gastrophagy will be addressed further in future work, but from the information presented here we can identify two of them. It seems likely that guts are consumed because meat is a preferred food (particularly by men) (Berbesque et al., 2011) and so is unlikely to be wasted. Guts are also consumed in part in the field for practical reasons; the intestines are often roasted at kill sites because they are quick to cook. Although the dietary importance of meat consumed at kill sites is largely under-studied in living forager groups (Berbesque et al., in review), much consideration has been given to the reasons why different parts of a carcass may be abandoned at a kill site, or taken back to camp in an ethnoarchaeological context (e.g., Binford, 1981, O'Connell, et al., 1988, Lupo, 2006). The treatment of the organs is usually overlooked, however, perhaps due to their failure to leave lasting archaeological traces. Despite this omission, it is useful to consider some of the factors that may play a part in decision making, such as the cost of transporting and processing parts, the taxonomy of the prey, the perceived rank of the part as a food item, the individual(s) involved in making the decisions, the size of the carrying party, the time of day a kill is make and the distance to camp, cooking technology, lack of storage, risks associated with hunting, seasonal and inter-annual variation in fat/muscle of prey, social influences and sharing obligations (O'Connell et al., 1988, Lupo, 2006). Given these many variables, and certainly others, it is not surprising that there is a great degree of variation in decision-making and it is not easy to predict what will be eaten at a kill site and what is taken back to camp in any given situation (O'Connell et al., 1988, Lupo, 2008). Similarly no one simple explanation for gut consumption is likely to be forthcoming. Based on ethnographic analogies from other foragers, there may also be reasons of taste or perceived health benefit, and these should be explored with the Hadza.

Potential benefits of gastrophagy to extinct warm-adapted hominins
The Hadza do not intentionally consume the chyme of their prey, only the guts themselves, although they do ingest the chyme in small quantities due to the processing techniques employed. However, given that other warm-adapted groups have been recorded as eating chyme (Silberbauer, 1981, O'Dea et al., 1991, Peterson & Walhof, 2002, Low, 2009) and chimpanzees have recently been shown to consume it preferentially (Krief et al., 2015), there is no reason to suppose that extinct tropical hominins would not have done so. As carnivory and hunting increased in hominin species (Ungar, 2004, Alemseged & Bobe, 2009), access to the stomachs of prey would have increased and chyme may have been targeted preferentially, resulting in several potential benefits.

The Expensive Tissue Hypothesis (Aiello & Wheeler, 1995) states that, as the brain and the digestive system are both metabolically expensive, increasing brain size over the course of human evolution led to gut reduction to avoid raising basal metabolic rate. This was achieved via a diet high in energy and low in processing cost, probably including more meat and marrow with the potential additions of nuts or tubers (Aiello & Wheeler, 1995). Aiello and Wheeler (1995) originally suggested that this dietary shift occurred with the advent of *Homo erectus*; however, more recent work has questioned the timing of some of the morphological and physiological peculiarities potentially associated with greater meat-eating (see Antón & Snodgrass, 2012 and Pontzer, 2012 for reviews). Rather than the abrupt change of ecological niche in *H. erectus* originally envisaged, a more complex picture has now emerged, with changes in body mass, encephalisation, alterations in the pelvic and rib morphology suggesting a smaller gut, and life history changes occurring at different times and in different places (Antón & Snodgrass, 2012). In addition to the skeletal evidence, faunal analogies and dental analyses show greater meat consumption in *H. erectus* compared to contemporary *Paranthropus* and earlier *Australopithecus afarensis* (Ungar, 2004, Alemseged & Bobe, 2009). These data suggest a gradual change in diet and energy in-take over the course of human evolution (Antón & Snodgrass, 2012).

Wrangham and Carmody (2010) expanded on the Expensive Tissue Hypothesis, taking Aiello and Wheeler's (1995) suggestion that cooking could have been responsible for later encephalisation in the human lineage in the Middle Pleistocene, and placing it earlier. Wrangham and Carmody (2010) see biological adaptation to the control of fire and cooked food as the key innovation in human evolution. They ascribe many of the anatomical, biological, life history and behavioural differences between human and non-human primates, and between *H. erectus* and preceding australopithecines/early *Homo* to a "biological [commitment] to a cooked diet" (2010: 189). Humans are inefficient at processing major nutritional molecules (such as starch and protein) and cooking softens food, increasing fracturing. This decreases processing time and increases digestibility (Wrangham & Carmody, 2010). Cooking increases the net caloric gain, which has a direct effect on female reproductive success as well as allowing more energy to be devoted to brain growth (Wrangham & Carmody, 2010). Critics have argued that, despite the wealth of morphological (although, see above), ethnographic and physiological evidence to support Wrangham et al.'s arguments, there is little archaeological evidence for the habitual control of fire until the later Middle Pleistocene (Shimelmitz et al., 2014, Sorensen et al., 2014). This pushes forward the time-frame for these effects of cooking on human evolution to the era of late *H. heidelbergensis* and its successors.

Chyme is partly digested by the animal from which it comes, thus its digestion costs to the consumer may be cut and net energy gain raised, in a manner similar to cooking, leading to similar advantages to those proposed by Wrangham and Carmody (2010). If the chyme is from a herbivore with a specialized digestion system and microbiota capable of digesting chitin and cellulose, which humans cannot, this provides additional benefits in enabling access to otherwise inedible plant species. Counter-intuitively, therefore, the plant material in chyme may have been a key part of the beneficial role that meat had in early human evolution and, in addition to other possible processing techniques such as cooking, hominins may have gained

from getting something else to do the hard work of chewing and part-digesting their vegetable foods for them.

Above and beyond the potential energy/processing advantages of chyme consumption for hominins as a whole, gastrophagy could have played a particular role in the diet of the young and the old. Chyme could potentially have been used as a ready-made baby food that was easy for weanlings to process and digest. Earlier weaning facilitates mothers' return to reproductive cycling and food production. This shortens interbirth intervals (IBIs) and enables more offspring to be supported, in addition to the more direct link between energy gain, BMI and mothers' reproductive success (Wrangham and Carmody, 2010). Tooth loss in old age is associated with higher levels of mortality, when other criteria are controlled for, thus the availability of foods which require little mastication can contribute to longevity (Wrangham & Carmody, 2010). As such a food, chyme could plausibly have facilitated alloparent provisioning (often performed by older relatives [Hawkes et al., 1998, Kaplan et al., 2000]), potentially contributing to the reduction of IBIs seen in humans compared to other primate species (Wells and Stock, 2007) and increasing levels of reproductive success. In addition to their potential role in provisioning weanlings, older members of a community may retain important ecological knowledge invaluable in environmental conditions, such as drought, that occur infrequently. They may also contribute to the groups' food production with tasks such as extractive foraging long after more energy-expensive tasks become impossible (Wrangham & Carmody, 2010).

In addition to raised energy requirements during pregnancy and lactation, mothers and foetuses require additional micronutrients (Hockett & Haws, 2003; Allen, 2005; Berti, et al., 2011; Hockett, 2012). Particularly crucial micronutrients include B vitamins, vitamin A, D, iron, calcium and iodine (Allen, 2005; Berti et al., 2011). Micronutrient deficiency in the mother at any stage from periconception through to weaning can lead to reduced fertility and adverse pregnancy outcomes such as preterm delivery, miscarriage and still births, increased maternal mortality and preeclampsia (B vitamins, vitamin A, vitamin D, iron, iodine, calcium) or developmental problems for the child, including neural defects (folate, iodine, iron), low birth weight (iron), poor skeletal growth and dental mineralisation (vitamin D, calcium) and behavioural and mental abnormalities (iron, iodine) (Allen, 2005: Berti et al., 2011). Over the long term, deficiency in micronutrients such as vitamin D during gestation is also thought to increase susceptibility to common diseases. (Berti et al., 2011). For all these reasons, a diverse diet with a wide range of micronutrients are necessary for reproductive success.

To our knowledge, there is no detailed analysis of the micronutrient composition of organs or chyme in tropical species likely to have been available to extinct hominins in Africa. However, there is some data of relevance to hominin species such as Neanderthals and *H. antecessor* living in more temperate climates. Reindeer stomach and bearded seal intestines are both sources of vitamin A, calcium, iron and zinc in the traditional Inuit diet (Andersen, 2005). Of these micronutrients, both are particularly high in calcium. They are two of the richest sources

of this micronutrient studied in Andersen's (2005) comprehensive study of 39 species broken down into (depending on what parts are eaten of that species) nutritional values for muscle, liver, blubber, kidney, eyes, brain, flippers, heart, fat, oil, intestines, bone marrow, lungs, stomach, tongue, berries, leaves, stem or buds. Further to the benefits of consuming the organs themselves, as suggested above the chyme of herbivores as a scarce vegetable food source in plant poor regions is likely to have been nutritionally as well as energetically beneficial to pregnant and nursing mothers. Plant foods such as leafy vegetables are rich in vitamin A precursors, which are vital in foetal visual, immune system and lung development (Berti et al., 2011) and compared to terrestrial mammals (muscle and organs), shellfish, birds and fish, plants have relatively high levels of vitamin A, vitamin D and calcium (Hockett & Haws, 2003). Carbohydrates from vegetable foods are also important during pregnancy and lactation, not only due to increased energy demands, but because high levels of protein block calcium absorption (Hockett, 2012). Gastrophagy is therefore likely to have been particularly beneficial during pregnancy and lactation when requirements for calcium and other micronutrients is greater.

Potential implications of gastrophagy for palaeodietary reconstructions
The practice of gastrophagy in the Hadza highlights the need to consider the possible effects of secondarily consumed (i.e., via gastrophagy) plant material. If sample sizes are very small, as is common when dealing with fossil species, relatively few plant remains could potentially confuse interpretations of diet using methods such as calculus analysis. Further investigation should be carried out into whether such practices might also potentially confound other methods such as microwear and isotope analyses. For example, the possibility should be investigated that chyme, originating from a higher higher trophic level than primarily ingested plant food, could enrich isotopic Nitrogen signals and confuse dietary interpretations. This would be analogous with what is seen in nursing infants, who show enriched Nitrogen signals compared to their mothers (Fuller, 2006, Humphrey, 2014).

A theoretical example of a case where gastrophagy could influence dietary reconstructions is *Australopithecus sediba*, which appears to have an extremely unusual diet for a hominin, including bark and leaves (Henry et al., 2012). It is pertinent to consider what effect the consumption of chyme from a bark-eating animal, such as a vervet monkey (Tournier et al., 2014) or porcupine (Kingdon, 1997), could have on the reconstruction of *A. sediba*'s diet. Henry and her colleagues are leaders in this field and used several different methods (calculus, microwear and isotope analyses) to infer diet in this species; it is not our intention to imply that they are incorrect in their conclusion, merely to use *A. sediba* as an interesting example of how secondary sources of plant remains could be important in palaeoanthropological analyses.

Other potentially confounding sources of plant material
In addition to the potentially confounding effects of gastrophagy, there are other ways in which plant material could be unintentionally consumed by foragers. As Speth (2012) points out, the simplest and earliest vessels for transporting and heating liquids were probably animal organs,

such as the stomach, and plant remains are likely to have remained adhering to the inside of such vessels after butchery and during use. Among the Hadza, after butchering an animal, men's hands and lower arms are often covered in dried and drying blood. To wash off such blood, men will in some instances use the still-damp contents of the stomach. It is easy to imagine how this might then lead to transference of some plant remains to the mouth during eating (see Figure 1).

Even if they are not eaten, plant remains from herbivore guts should be considered as a possible contaminant in reconstructions of diet. Transport of carcasses to living sites for processing and consumption could lead to plant remains in sediment, which could be misinterpreted as evidence of plant foods (e.g., Madella et al., 2002). In this context, charred plant remains could also be due to cooking guts, rather than cooking the plants themselves as the primary focus as food (e.g., Lev et al., 2005). Plant materials recovered from residue on stone tools could also confuse dietary and behavioural reconstructions if the plant remains originate from the butchering of an animal and cutting through guts, and these are then interpreted as the consequence of plant processing. It is certainly not our intention to suggest that fossil hominins were not exploiting plant resources (see also Buck & Stringer, 2014), merely to caution that herbivore guts and gut contents should be considered when the archaeological and anthropological evidence is interpreted.

Conclusions

The frequency and range of gastrophagy reported in the ethnographic record suggests that this is a human practice with a long history. Although clear benefits can be seen for boreal and cold-adapted recent *H. sapiens* and extinct hominins, such as Neanderthals and the Happisburgh hominins, the context for gastrophagy in warm environments is poorly known. Here we present preliminary data from a group of extant foragers who practice gastrophagy, the Hadza. We can conclude from these initial investigations that gastrophagy is a common and frequent (though seasonally variable) part of the Hadza diet, particularly for men, given the larger meat component of their diets. Further investigation into the reasons for Hadza gastrophagy are necessary, in addition to more comprehensive data on the contribution of small prey and animal foods eaten out of camp. Comparisons with other foragers would be of interest particularly, if possible, in groups that consume chyme as well as the guts themselves. Since few people today subsist exclusively on forager diets, these investigations may be limited by what is available in the ethnographic record, and this highlights the importance of the 'real time' information from the Hadza, as presented here.

We believe that gastrophagy would have been an additional benefit to the often cited importance of increased carnivory to extinct hominins in Africa. We see the practice in a complementary (and possibly earlier) role to cooking in optimizing improved dietary energy gain/metabolic cost ratios enabled by increases in meat eating. Gastrophagy may have contributed to the energy surplus that enabled encephalisation in our lineage. We suggest that, if gastrophagy can be expected to have been practiced by fossil hominins, as suggested by analogies to extant and recent human foragers living in similar environments as well as to

chimpanzees, we must consider its potential influence on analyses of plant evidence from hominin remains, archaeological sites and archaeological remains.

The data and knowledge of relevance to a single research question are often encased within different disciplines; our experiences in investigating gastrophagy show the importance of social anthropologists, evolutionary biologists, palaeoanthropologists and archaeologists sharing their expertise in interdisciplinary collaborations.

References

Aiello, L. C., & Wheeler, P. 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* 36: 199-221.

Alemseged, Z. & Bobe, R. 2009. Diet in early hominin species: a paleoenvironmental perspective. In Hublin, J. –J. & Richards, M. P. (Eds.). *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Pp 181-188. Springer Science & Business: Dordrecht.

Allen, L. H. 2005. Multiple micronutrients in pregnancy and lactation: an overview. *The American Journal of Clinical Nutrition* 81: 1206S-1212S.

Andersen, S. A. 2005. Vitamins and minerals in the traditional Greenland diet. In: National Environmental Research Institute (Ed.). *NERI Technical Report Number 528*. National Ministry of the Environment, Copenhagen.

Antón, S. C. & Snodgrass, J. J. 2012. Origins and evolution of genus *Homo*. *Current Anthropology* 53 (S6): S479-S496.

Ashton, N., Lewis, S. G., De Groote, I., Duffy, S. M., Bates, M., Bates, R., Hoare, P., Lewis, M., Parfitt, S. A., Peglar, S., Williams, C. & Stringer, C. 2014. Hominin footprints from Early Pleistocene deposits at Happisburgh, UK. *Public Library of Science ONE* 9: e88329.

Berbesque, J. C. and Marlowe, F. W. 2009. Sex differences in food preferences of the Hadza hunter-gatherers. *Evolutionary Psychology* 7, 601-616.

Berbesque, J. C., Marlowe, F. W., Crittenden, A. N. 2011. Sex differences in Hadza eating frequency by food type. *American Journal of Human Biology*. 23, 339-345.

Berbesque, J. C., Wood, B., Crittenden, A. N., Mabulla, A., Marlowe, F. W., ND. Gatherer-hunters: Hadza men's self provisioning while on walkabout.

Berger, G. W., Pérez-González, A., Carbonell, E., Arsuaga, J. L., Bermúdez de Castro, J. -M. & Ku, T. -L. 2008. Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain, *Journal of Human Evolution* 55: 300-311.

Berti, C., Biesalski, H. K., Gärtner, R., Lapillone, A., Petrzik, K., Poston, L., Reman, C., Koletzko, B. & Cetin, I. 2011. Micronutrients in pregnancy: current knowledge and unresolved questions. *Clinical Nutrition* 30: 689-701.

Binford, L .R. 1981. *Bones: Ancient Men and Modem Myths*. New York: Academic Press.

Buck, L. T. & Stringer, C. B. 2014. Having the stomach for in: a contribution to Neanderthal diets? *Quaternary Science Reviews* 96: 161-167.

Bunn, H. T., Gurtov, A. N., 2014. Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. *Quaternary International*, 322, 44-53.

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. *American Journal of Clinical Nutrition* 71: 682-6982.

Crittenden, A. N., Conklin-Brittain, N. L., Zes, D. A., Schoeninger, M. J., & Marlowe, F. W., 2013. Juvenile foraging among the Hadza: Implications for human life history. *Evolution and Human Behaviour*, 34, 299-304.

Falguères, C. 2003. ESR dating and the human evolution: contribution to the chronology of the earliest humans in Europe. *Quaternary Science Reviews* 22: 1345-1351.

Fediuk, K. 2000. *Vitamin C in the Inuit diet: past and present.* MSc. Thesis, McGill University.

Fuller, B. T., Fuller, J. L., Harris, D. A. & Hedges, R. E. M. 2006. Detection of breastfeeding and weaning in modern human infants with Carbon and Nitrogen stable isotope rations. *American Journal of Physical Anthropology* 129: 279-293.

Hardy, B. L., Kay, M., Marks, A. E., Monigal, K. 2001. Stone tool function at the Paleolithic sites of Starosele and Buran Kaya III: behavioural implications. *Proceedings of the National Academy of Sciences USA* 98: 10972-70977.

Hardy, K., Buckley, S., Collins, M. J., Estalrrich, A., Brothwell, D., Copeland, D., GarcÍa-Tabernero, A., GarcÍa-Vargas, S., de la Rasilla, M. Lalueza-Fox, C. Huguet, E., Bastir, M., Santamaría, D., Madella, M., Wilson, J. Fernández Cortés, Á. & Rosas, A. 2012. Neanderthal medics? Evidence for food, cooking and medicinal plants entrapped in dental calculus. *Naturwissenschaften* 99: 617-626.

Hardy, K., Buckley, S. & Huffman, M. 2013. Neanderthal self-medication in context. *Antiquity* 87: 873-878.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Oftedal, O. T., & Blumenschine, R. J., 1991. Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 334, 243-251.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H. & Charnov, E. L. 1998. Grandmothering, menopause and the evolution of human life history strategies. *Proceedings of the National Academy of Sciences USA* 95: 1336-1339.

Hawkes, K., O'Connell, J. F., Jones, N. B., 2001. Hadza meat sharing. *Evolution and Human Behavior*. 22, 113-142.

Henry, A. G., Brooks, A. S. & Piperno, D. R. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proceedings of the National Academy of Sciences USA* 108: 486-491.

Henry, A. G., Ungar, P. S., Passey, B. H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P. De Ruiter, D. J. & Berger, L. 2012. The diet of *Australopithecus sediba*. *Nature* 487: 90-92.

Henry, A. G., Brooks, A. S. & Piperno, D. R. 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. *Journal of Human Evolution* 69: 44-54.

Hockett, B. 2012. The consequences of Middle Paleolithic diets on pregnant Neanderthal women. *Quaternary International* 264: 78-82.

Hockett, B. & Haws, J. 2003. Nutritional ecology and diachonic treds in Paleolithic diet and health. *Evolutionary Anthropology* 12: 211-216.

Huffman, M. A. 2003. Animal self-medication and ethnomedicine: exploration and exploitation of the medicinal properties of plants. *Proceedings of the Nutrition Society* 62: 371-381.

Humphrey, L. T. 2014. Isotopic and trace element evidence of dietary transitions in early life. *Annals of Human Biology* 41: 348-357.

Hylander, W. L., 1975. The adaptive significance of Eskimo craniofacial morphology. In: A. A. Dahlberg and T. M. Graber (Eds.). *Orofacial growth and development.* Walter De Gruyter Inc.: Berlin. pp. 129–169.

Kaplan, H. S., Hill, K., Lancaster, J. B., Hurtado, A. M. 2000. A theory of human life history evolutionL diet, intelligence and longevity. *Evolutionary Anthropology* 9 : 156-183.

Kelly, R. L. 2013. *The Lifeways of Hunter-gatherers : the Foraging Spectrum*. Cambridge University Press : Cambridge.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. Academic Press: San Diego.

Krief, S., Daujeard, C., Moncel, M.-H., Lamon, N. & Reynolds, V. 2015. Flavouring food: the contribution of chimpanzee behaviour to the understanding of Neanderthal calculus composition and plant use in Neanderthal diets. *Antiquity* 89: 464-471.

Krueger, K. L., & Ungar, P. S. 2012. Anterior dental microwear texture analysis of the Krapina Neandertals. *Central European Journal of Geosciences* 4: 651-662.

Kuhnlein, H. V. & Turner, N. J. 1991. *Traditional plant foods of Canadian indigenous peoples: nutrition, botany and use.* Food and Nutrition in History and Anthropology*. Vol. 8. Gordon and Breach Scientific Publishers: Philadelphia.

Kumlien, L. 1880. Ethnology. Fragmentary notes on the Eskimo of Cumberland Sound III. *Science* 1: 214-218.

Lalueza-Fox, C., Gigli, E., de La Rasilla, M., Fortea, J., Rosas, A., 2009. Bitter taste perception in Neanderthals through the analysis of the TAS2R38 gene. *Biology Letters* 5: 809-811.

Lame Deer, J. D. & Erdoes, R. 1972. *Lame Deer: Seeker of Visions*. Simon & Schuster: New York.

Leach, J. 2013. Gut microbiota: please pass the microbes. *Nature* 504: 33.

Lev, E., Kislve, M. E. & Bar-Yosef, O. 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. *Journal of Archaeological Science* 32: 475-484.

Low, C. 2009. Birds in the life of KhoeSan; with particular reference to healing and ostriches. *Alternation: the Interdisciplinary Journal of the Study of the Arts and Humanities in South Africa*. 16: 64-90.

Lupo, L. K. 2006. What explains the carcass field processing and transport decisions of contemporary hunter-gatherers? Measures of economic anatomy and zooarchaeological skeletal part representation. *Journal of Archaeological Method and Theory* 13: 19-66.

Madella, M., Jones, M. K., Goldberg, P., Goren, Y. & Hovers, E. 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): the evidence from phytolith studies. *Journal of Archaeological Science* 29: 703-719.

Mabey, R. 1973. *Food for Free: A Guide to the Edible Wild Plants of Britain.* Collins: London.

Marlowe, F. W., Berbesque, J. C. 2009. Tubers as fallback foods and their impact on Hadza hunter-gatherers. *American Journal of Physical Anthropology* 140: 751-758.

Marlowe, F. 2010) *The Hadza: hunter-gatherers of Tanzania* (Vol. 3). Univ of California Press.

Marlowe, F. W., Berbesque, J. C., Wood, B., Crittenden, A. N., Porter, C. 2014. Honey, Hunter-gatherers, Hadza, and Human Evolution. *Journal of Human Evolution* 71: 119-128.

Nozedar, A. 2012. *The Hedgerow Handbook: Recipes, Remedies and Rituals.* Square Peg: London.

Parfitt, S. A., Ashton, N. M., Lewis, S. G., Abel, R. A., Coope, G. R., Field, M. H., Gale, R., Hoare, P. G., Larkin, N. R., Lewis, M. D., Karloukovski, V., Maher, B., Peglar, S. M., Preece, R. C., Whittaker, J. E. & Stringer, C. B. 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466: 299-233.

Perry, G. H., Kistler, L., Kelaita, M. A. & Sams, A. J. 2015. Insights into hominin phenotypic and dietary evolution from ancient DNA sequence data. *Journal of Human Evolution* 79: 55-63.

Peterson, D. R. & Walhof, D. R. 2002. Rethinking Religion. In Peterson, D. R. & Walhof, D. R. *The Invention of Religion: Rethinking Belief in Politics and History*. Rutgers University Press: Piscataway. Pp. 1-18.

Pontzer, H. 2012. Ecological energetic in early *Homo*. *Current Anthropology* 53 (S6): S346-S358.

Power, R. C., Salazar-GarcÍa, D. C., Wittig, R. M. & Henry, A. G. 2014. Assessing use and suitability of scanning electron microscopy in the analysis of micro remains in dental calculus. *Journal of Archaeological Science* 49: 160-169.

Power, R. C., Salazar-García, D. C., Straus, L. G., González Morales, M. R. & Henry, A. G. 2015. Microremains from El Mirón Cave human dental calculus suggest a mixed plant–animal subsistence economy during the Magdalenian in Northern Iberia. *Journal of Archaeological Science* 60: 39-46.

O'Dea, K., Jewell, P. A., Altmann, S. A., Strickland, S. S. Oftedal, O. T. 1991. Traditional diet and food preferences of Australian hunter-gatherers. *Philosophical Transactions of the Royal Society London Biological Sciences* 34: 233-241.

O'Connell, J. F., Hawkes, K. & Burton Jones, N. 1988. Hadza hunting, butchering and bone transport and their archaeological implications. *Journal of Anthropological Research* 44: 131-161.

Schnorr, S. L., Candela, M., Rampelli, S., Centanni, M., Consolandi, C., Basaglia, G., Turroni, S., Biagi, E., Peano, C., Severgnini, M., Fiori, J., Gotti, R., De Bellis, G., Luiselli, D., Brigidi, P., Mabulla, A., Marlowe, F., Henry, A. G., Crittenden, A. N., 2014. Gut microbiome of the Hadza hunter-gatherers. *Nature Communications* 5: 1-12.

Shimelmitz, R., Kuhn, S. L., Jelinek, A. J., Ronen, A., Clark, A. E., & Weinstein-Evron, M. 2014. Fire at will: The emergence of habitual fire use 350,000 years ago. *Journal of Human Evolution* 77: 196-203

Silberbauer, G. 1981. Hunter/Gatherers of the Central Kalahari. In: Harding, R. S. O. & Geza T. (Eds.). *Omnivorous Primates: Gathering and Hunting in Human Evolution*. Columbia University Press: New York. Pp. 455-498.

Sistiaga, A., Mallol, C., Galván, B. & Everett Summons, R. 2014. The Neanderthal meal: a new perspective using faecal biomarkers. *Public Library of Science ONE* 9: e101045.

Smith, F. H., 1976. Behavioral interpretation of changes in craniofacial morphology across the archaic/modern *Homo sapiens* transition. In: E. Trinkaus (Eds.). *The Mousterian Legacy.* Archaeopress: Oxford. Pp. 46-56.

Sorensen, A., Roebroeks, W., & van Gijn, A. 2014. Fire production in the deep past? The expedient strike-a-light model. *Journal of Archaeological Science* 42: 476-486.

Speth, J. D., Widdowson, E. M., Oftedal, O. T., Foley, R. A., & Van Soest, P. 1991. Protein Selection and Avoidance Strategies of Contemporary and Ancestral Foragers: Unresolved Issues [and Discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 334: 265-270.

Speth, J. D. 2012 Middle Palaeolithic subsistence in the Near East: zooarchaeological perspectives – past, present and future. *Before Farming* 2: 1-45.

Tournier, E., Tournier, V., Waal, E., Barrett, A., Brown, L., & Bshary, R. 2014. Differences in diet between six neighbouring groups of vervet monkeys. *Ethology*, 120: 471-482.

Ungar, P. 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo. Journal of Human Evolution* 46: 605-622.

van Zyl, L. & Ferreira, A. V. 2004. Physical and chemical carcass composition of springbok (*Antidorcas marsupialis*), blesbok (*Damaliscus dorcus phillipsi*) and impala (*Aepyceros melampus*). *Small Ruminant Research* 53: 103-109.

Wells, J. C. K. & Stock, J. T. 2007. The Biology of the colonizing ape. *Yearbook of Physical Anthropology* 50: 191-222.

Wood, B. M. and Marlowe, F. W. (2013). Household and kin provisioning by hadza men. *Human Nature,* 24, 280-317.

Wood, B. M. and Marlowe, F. W. (2014a). Toward a reality-based understanding of hadza men's work: A response to hawkes et al. (2014). *Human Nature,* 25, 620-630.

Wood, B. M., Pontzer, H., Raichlen, D. A. and Marlowe, F. W. (2014b). Mutualism and manipulation in hadza-honeyguide interactions. *Evolution and Human Behavior,* 35, 540-546.

Woodburn, J. 1979. Egalitarian societies. *Man* 17: 431-451.

Wrangham, R. & Carmody, R. 2010. Human adaptation to the control of fire. *Evolutionary Anthropology* 19: 187-199.