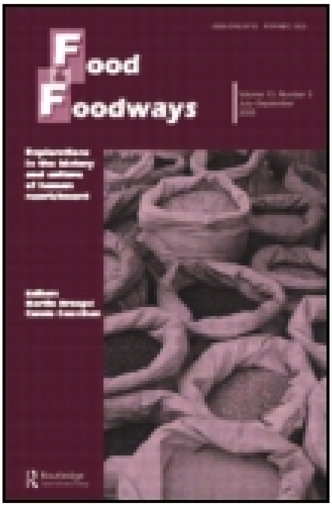

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The Importance of Honey Consumption in Human Evolution

Alyssa N. Crittenden [a]

[a] Department of Anthropology , University of Nevada , Las Vegas, Nevada, USA

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The Importance of Honey Consumption in Human Evolution

ALYSSA N. CRITTENDEN
Department of Anthropology, University of Nevada, Las Vegas, Nevada, USA

It has been suggested that honey may have been an important food source for early members of the genus Homo*, yet the importance of meat and savanna plant foods continue to be stressed as the most relevant foods in dietary reconstructions. Here, the importance of honey and bee larvae in hominin diets is explored. Ethnographic reports, examples of Paleolithic rock art, and evidence from non-human primates are used to show that early hominins likely targeted beehives using the Oldowan tool kit. The consumption of honey and bee larvae likely provided significant amounts of energy, supplementing meat and plant foods. The ability to find and exploit beehives using stone tools may have been an innovation that allowed early* Homo *to nutritionally out-compete other species and may have provided critical energy to fuel the enlarging hominin brain.*

Honey is one of the most energy-dense foods in nature (Skinner 1991), but despite suggestions that it may have been an important food source for early *Homo* (Allsop and Miller 1996; Bunn and Schoeninger 2009; McGrew 2001; Schoeninger et al. 2003; Skinner 2001), it has received little attention in most reconstructions of early hominin[1] diet composition. While the importance of meat (Bunn 2007; Cordain et al. 2001; Eaton et al. 1998; Stanford and Bunn 2001) and savanna plant foods, e.g., underground storage organs (USOs) (Dominy et al. 2008; Hawkes et al. 1997; Wrangham et al. 1999), are routinely highlighted, the importance of honey and larvae consumption have been largely overlooked.

The appearance of Oldowan tool technology, the earliest assemblages of deliberately flaked stone artifacts, coupled with the spread of grasslands[2]

Address correspondence to Alyssa N. Crittenden, Department of Anthropology, University of Nevada, Las Vegas, 4505 S. Maryland Parkway, Las Vegas, NV 89154-5003. E-mail: alyssa.crittenden@unlv.edu

across East Africa, suggest that ecological changes during the Late Pliocene may have led to changes in resource availability for early *Homo* (Ungar et al. 2006). An expanded toolkit would have allowed early hominins to target, process, and consume a greater range of foods than was previously available (Dominguez-Rodrigo et al. 2001; Shea 2007; Ungar et al. 2006). Stable carbon isotope data of hominin tooth enamel and faunal reconstructions suggest that early hominins fed in an open country savanna woodland habitat (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005). Although the general consensus agrees that environmental changes along with technological innovation provided an opportunity for major dietary shifts, the types of foods that would have been targeted remain unclear (Leonard et al. 2007; Ungar et al. 2006). Here, the probable importance of honey and bee larvae in early hominin diet is explored. Nutritional composition, ethnographic reports, examples of Paleolithic rock art, and evidence from non-human primates are used to show that early *Homo* was capable of, and likely benefited from, targeting beehives using the Oldowan tool kit. Liquid honey may have provided much-needed energy to early hominin foragers and would have been an important supplement to meat and plant collection.

SEASONAL PRODUCTION AND NUTRITIONAL COMPOSITION OF HONEY AND LARVAE

The seasonality of honey production differs in temperate versus tropical climates. In temperate zones, the production cycle of both stinging (*Apis mellifera*) and stingless (*Meliponinae*) honeybees is highly seasonal (Crane 1990). In tropical zones, honeybees are dependent upon rainfall, regardless of the season; during relatively wet years, production of honey may be continual, whereas in dry years, production may be restricted to short periods following a rain (Crane 1990, 1999).

Liquid honey, both wild and domestic, contains approximately 80–95 percent sugar and is a concentrated source of fructose and glucose (Bogdanov et al. 2008; Murray et al. 2001; White et al. 1962). Honey also contains trace amounts of several essential vitamins and minerals (Iskander et al. 1995; Terrab et al. 2004) and contains components that act as preservatives, including a-tocopherol, ascorbic acid, flavonoids, glucose oxidase, catalase, and peroxidase (Crane 1975; Ferreres et al. 1993; Nagai et al. 2006). Although only small amounts of protein (mainly free amino acids) are found in liquid honey (Bogdanov et al. 2008), wild honeys contain higher levels of protein and fat, most likely because they contain trace amounts of bee larvae, whereas cleaned and commercially processed honey does not (Murray et al. 2001). Bee larvae is a good source of protein, fat, several essential minerals, and B-vitamins (Finke 2005). Combined, honey and bee larvae are excellent sources of energy, fat, and protein and represent high-quality food sources that have been targeted for much of human history.

THE ROCK ART OF HONEY COLLECTION

Multiple examples of Upper Paleolithic (40,000–8,000 years ago) rock art linked to honey and bees are found in Spain, India, Australia, and Southern Africa. The most abundant rock art representations of honey related activities in Europe are found in Spain. Paintings in a side chamber of the Altamira cave (Figure 1), dated to roughly 25,000 years ago (Pager 1976), depict

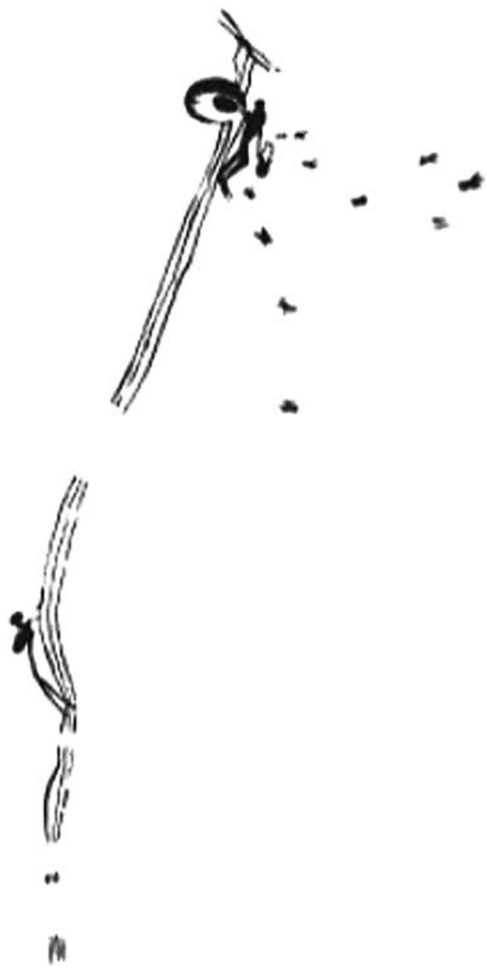

FIGURE 1 Mesolithic rock painting of honey collection from a wild bee nest, La Araña shelter, Valencia, Spain. Reprinted from Crane 1999, with permission from International Bee Research Association (IRBA).

honeycomb, bees, and honey collection ladders (Cartailhac and Breuil 1906). In an open-air rock shelter in Bicorp in the Valencia Province, depictions of honey collection, bee swarms, and comb representations, dating to 10,000 years ago, have been found (Dams 1978; Hernández-Pacheco 1928). Multiple representations of honey collection have been found in central India. Images include groups of both men and women sitting in trees containing beehives, smoking hives, and climbing ladders to access honeycombs (Gordon 1960; Mathpal 1984). There are also drawings of basketlike objects that may represent dried-out gourds for collecting liquid honey (Mathpal 1984). In Australia, rock art depicting the nests of stingless bees have been found near Darwin (Crane 1975) and near the Laura River (Trezise 1973). Figures made with beeswax, dated to 4,000 years ago, have been found on the walls of open rock shelters in the Northern Territory (Nelson 1995).

The majority of rock paintings depicting honey collection and bee-related topics are located in Africa (Crane 1986, 1999). In South and West Africa (Johnson et al. 1959; Rudner and Rudner 1970), Zambia (Clark 1942), Namibia (Crane 1983), and Lesotho (Smits 1971), there are depictions of bee swarms, hives, and people on ladders accessing honeycomb, represented as ovoid shapes with black and white coloration (Pager 1973; Woodhouse 1989). The dark shaded areas represent comb filled with honey or pupae, and the light areas represent empty comb decorated with dots representing visible larvae in uncapped cells (Crane 1983). A depiction of a figure smoking a beehive (date unknown) was found in Toghwana Dam, Zimbabwe (Figure 2). The San foragers claim that their people have used this cave for approximately 10,000 years (Crane 1999).

The abundance of rock art depicting honey collection scenes at several sites throughout the world suggests that honey and larvae may have been an important part of the Paleolithic diet and daily life. It can be expected, however, that early hominins were exploiting beehives long before the practice was represented artistically; beehives and the stick tools used to access their contents do not survive the archaeological record. Data on the diet composition and food collection practices of foraging populations offer compelling evidence that honey and bee larvae may have contributed to a significant portion of the early *Homo* diet.

ETHNOGRAPHY OF HONEY CONSUMPTION

Honey and bee larvae consumption is widespread among human populations. A large body of literature reports the importance of honey in the diets of human foragers (Bodenheimer 1951); however, data on the amount collected and consumed remain largely anecdotal. Abundant consumption of honey and brood (larvae), both for stinging (*Apis mellifera*) and stingless

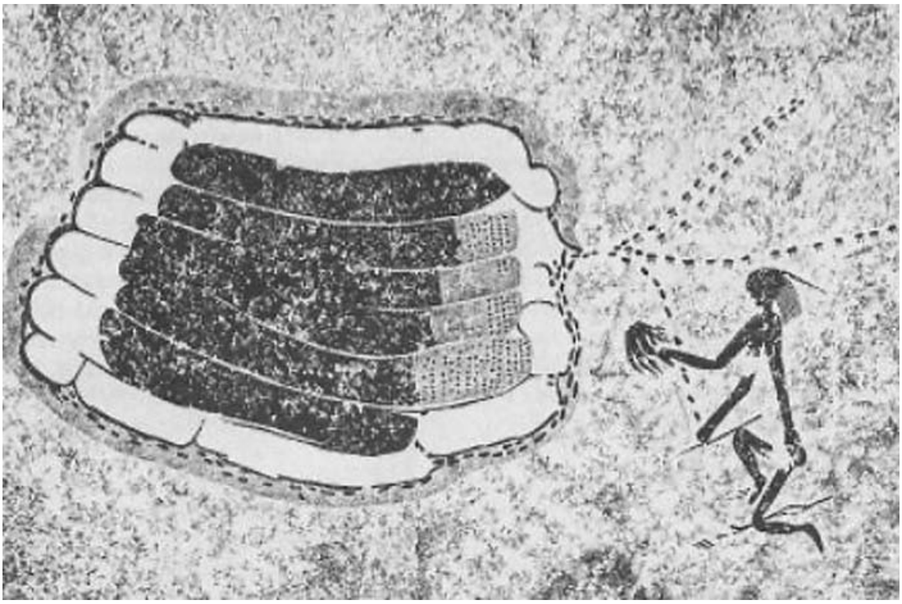

FIGURE 2 Rock painting of figure smoking a beehive, Toghwana Dam, Zimbabwe. Reprinted from Crane 1999, with permission from International Bee Research Association (IRBA).

bees (*Meliponinae*), is reported for foraging groups in Latin America, Asia, Australia, and Africa.

Across Latin America, multiple foraging groups focus a considerable amount of their collection effort on honey and bee larvae during distinct periods throughout the year (Ramos-Elorduy et al. 1997). The Yukpa-Yuko of Venezuela and Colombia consider bees the "single most important group of insects" in their diet (Ruddle 1973), and the Hiwi of Venezuela also consume significant amounts of both liquid honey and bee larvae during both the wet and the dry seasons (Gurven et al. 2000; Hill 2002; Hurtado and Hill 1987, 1990). The Ache of Paraguay consider honey and bee larvae to be the second most important resource class in their diet after large game meat (Hill et al. 1984; Kaplan and Hill 1985). The detailed data on the Ache quantifies the ways in which bees and their products contribute to overall diet composition. The energetic value of Ache honey is reported to be 3,232 calories per kilogram; consumption of honey and brood is, on average, 1,163 calories per person per day (Hurtado et al. 1985). Although honey is most abundant during the early part of the wet season, it is available in varying amounts throughout the year (Hill 2002; Hill et al. 1984; Hawkes et al. 1982).

In Asia, the honey foragers of Nepal target the nests of large stingless and stinging honeybees and collect approximately 40 liters of liquid honey and 10 kilograms of comb in less than one hour of foraging (Valli and Summers 1988). They utilize bamboo ladders to climb within reach of the nests, which are usually situated high in cliff crevices or in trees on the cliff face (Underwood 1990). The Tamang of Nepal (Masvie 2006; Thapa 2000) and the Onge of the Andaman Islands (Cipriani 1966; Crane 1975) also collect and consume large quantities of honey and bee larvae.

Various foraging peoples of Australia have historically utilized the hives of both honeybees and stingless bees, eating large amounts of honey and brood (Akerman 1979; O'Dea et al. 1991). Both the men and women of the Worora, Wunambal, and Ngarinjin tribes from west Australia are reported to have used digging sticks, hammer stones, and stone hatchets to gain access to beehives (Akerman 1979). The Wanindiljangwa of the north coast of Australia highly value the "sugar bag" (Worsley 1961), which contains honey, brood, and wax comb. The sugar bag is considered to be one of the most valued foods in their dietary repertoire and produces 1,680 calories per kilogram (Meehan 1977).

Reports on African foragers provide the most detailed accounts of honey collection and consumption. The ecology of the African environment, primarily miombo woodland and baobab trees, have bark that is highly suitable for hive construction and provide reliable honey throughout the year (Guy 1972). The various honey collection techniques across Africa include using climbing ropes to gain access to hives located high in trees, hammering pegs into the trunk of a tree to climb to the hive's location, or using smoke to stun the bees, which then fly out and abandon the hive and its contents (Bodenheimer 1951; Guy 1972; Crane 1999). Anecdotal references to honey collection and consumption are reported for various groups, including the Mikea of Madagascar (Tucker 2004), the Tongwe of Tanzania (Takeda 1976), and the Ogiek of Kenya (Nightingale 1983). There is quantified data available, however, on the amounts collected and consumed by the Efe foragers of the Ituri Forest in the Democratic Republic of the Congo and the Hadza foragers of Tanzania.

The Efe have a "honey season" that lasts from July–August (Terashima 1998). During this season, they move deep into the forest in search of the liquid honey and larvae of both stinging and stingless bees. During the honey season, they rely almost entirely on honey, brood, and pollen (Ichikawa 1981; Turnbull 1976). Men and women collect honey together in family groups and share their yield once they have returned to camp. The average amount of honey and brood collected by the average person per day is 3.32 kilograms, and the average amount consumed per person per day is 0.62 kilograms of honey (dry weight), which is calculated as 1,900 calories per day (Ichikawa 1981). Honey contributes roughly 70 percent of the diet by weight and 80 percent by calories (Ichikawa 1981; Terashima 1998), making it the largest component of the Efe diet during the wet season.

Among the Hadza foragers of Tanzania, honey is the most prized and highly ranked food source (Berbesque and Marlowe 2009). The Hadza collect the honey of stinging and stingless bees, consuming the larvae of both.

Honey comprises approximately 15 percent of the Hadza diet (Marlowe 2001), is shared widely outside of the household, and is consumed by the entire camp (Bunn and Schoeninger 2009; Marlowe 2003). Liquid honey is a primary weaning food[3] for Hadza children (Crittenden et al. n.d.). Male foragers are the primary honey collectors; however, children also routinely target beehives and return to camp with honey to share (Crittenden et al. n.d.). Young male foragers are able to collect and consume upwards of 3,000 kilocalories of honey during a three-hour foraging trip (Crittenden 2009). Honey is typically housed high off the ground in large baobab trees. Hadza men drive posts into the trunk of the tree, which the men and boys then climb in order to access the hive (Figure 3).

When locating an active hive, Hadza foragers often employ the assistance of the honey guide bird, *Indicator indicator*, a paleotropical near passerine bird that occupies sub-Saharan Africa (Short and Horne 2002). The honey guide is also an accomplice in assisting honey badgers

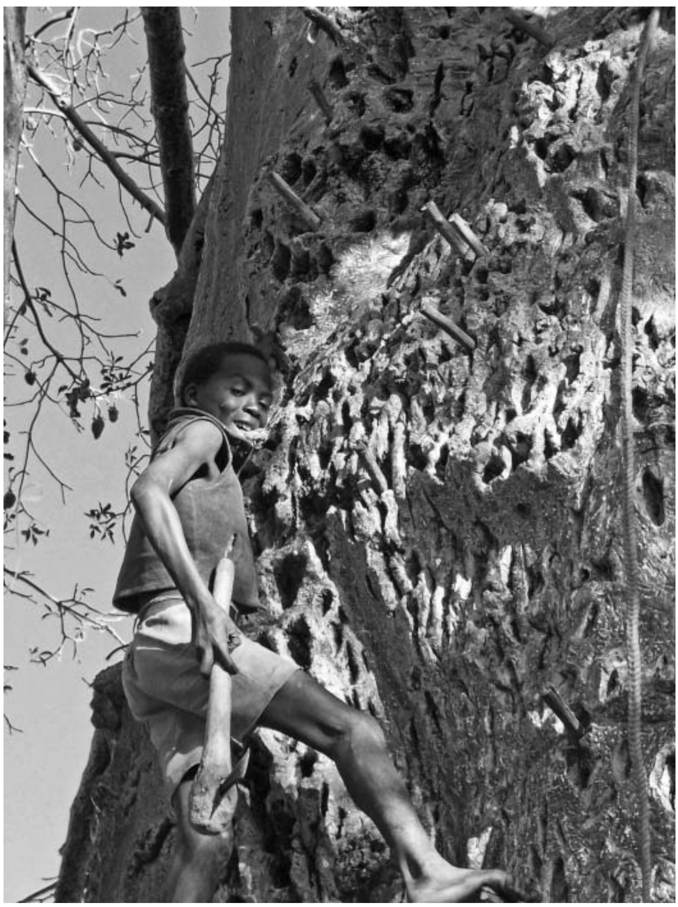

FIGURE 3 Hadza honey collection in large baobab tree.

(*Mellivora capensis)* and baboons (*Papio cynocephalus*) locate beehives (Dean and MacDonald 1981; Zimmerman et al. 1999). In the case of the Hadza, the honey guide bird leads the honey forager to the hive. They stay in constant communication via a series of chatters and whistles. When the forager reaches the hive, he chops into the tree to create a large hole and then typically smokes the bees. This involves placing burning brush in the mouth of the hive, which acts to reduce the electroantennograph response of the guard bees, who otherwise would release a volatile alarm odor pheromone called *iso-pentyl acetate* when threatened (Boch and Shearer 1962; Visscher et al. 1995). When the smoke enters the hive, the antennae receptors of the guard bees are dulled and they fail to sound the alarm. Smoking the hive also has the secondary effect of causing the other bees in the hive to gorge themselves on honey as a response to habitat threat. They take in vast amounts of honey and then vacate the hive in order to rebuild it elsewhere. When exposed to smoke, bees are dramatically less defensive and aggressive, and there is a negative correlation between degree of engorgement and the tendency to sting (Biamonte 1974; Conrad 1940; Free 1968; Visscher et al. 1995). The Hadza forager thus escapes getting stung by the bees, aptly named African killer bees, and extracts the contents of the hive (Figure 4). While he focuses on the liquid honey and larvae, the honey guide bird consumes the wax.

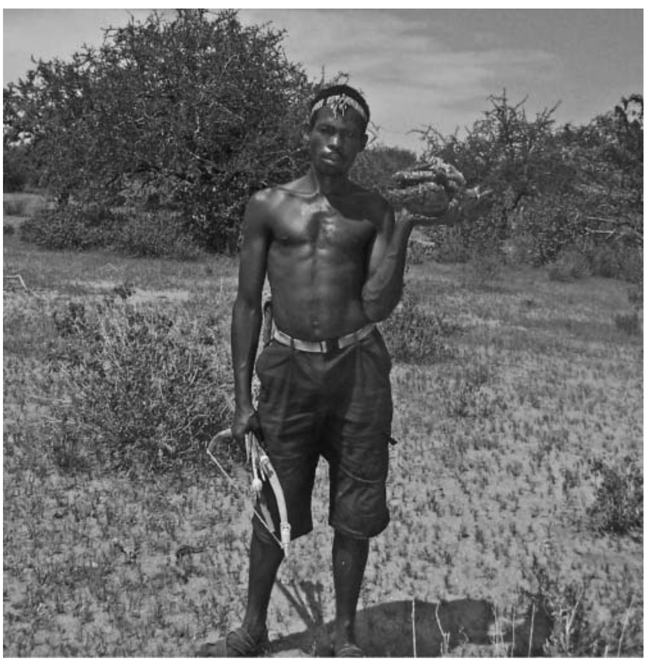

FIGURE 4 Hadza honey hunter with honey and bee larvae (*Apis mellifera adansonii*).

The above reports of honey and brood consumption represent only a subset of the populations who focus foraging efforts on the content of beehives. The ethnographic data outlined above are the most detailed and consistently reported examples representing the importance that honey plays in the diet of foraging populations.

HONEY COLLECTION BY NON-HUMAN PRIMATES

Several species of non-human primates are also successful honey collectors. Baboons and macaques routinely target the nests of both stinging and stingless bees (Botha 1970). In Bwindi Impenetrable National Park, baboons target the nests of stingless bees and harvest honey and larvae using their hands and muzzles (Kajobe and Roubik 2006). Gorillas also target honey in Bwindi (Kajobe and Roubik 2006; Stanford et al. 2000) and elsewhere (Botha 1970). Orangutans routinely collect honey and bees by using probes made of vegetation (Fox et al. 1998) or by smashing the hive (Rijksen 1978). Chimpanzees at many sites target honey and larvae using a variety of methods, including the use of stick tools to extract the contents of the hive (Central African Republic: Fay and Carroll 1994; Hicks et al. 2005; Côte d'Ivoire: Boesch and Boesch 1990; Gabon: Boesch et al. 2009; Tutin and Fernandez 2005; Gambia: Brewer and McGrew 1990; Nigeria: Fowler and Sommer 2007; Republic of Congo: Bermejo and Illera 1999; Sanz and Morgan 2009; Yamagiwa et al. 1988; Senegal: Bermejo et al. 1989; Tanzania: Goodall 1986; Uganda: Stanford et al. 2000; Kajobe and Roubik 2006; Watts 2008). Studies of chimpanzee tool use and diet composition are useful in models of early hominin behavior, not only because of their phylogenetic proximity to humans, but also because of their behavioral and anatomical similarities to our species. These data from non-human primates suggest that honey and larvae consumption may have been an important part of the subsistence strategy of early hominins.

DISCUSSION AND CONCLUSIONS—HONEY IN HUMAN EVOLUTION

Using the convergent evidence of honey and larvae consumption from non-human primates, historical and contemporary foraging populations, and artistic representations from Upper Paleolithic rock art, it can be expected that early hominins likely targeted beehives using the Oldowan tool kit.

It is possible that honey extraction was practiced by the Australopithecines, yet digging sticks do not survive the archaeological record. Oldowan stone tools begin to appear in the archaeological record approximately 2.5 mya in Africa (Semaw 2006; Toth and Schick 2009) and have also been found at multiple sites in Europe and Asia (Toth and Schick 2009). Using the Oldowan toolkit to split open beehives would have made honey and larvae more easily accessible and possibly allowed hominin foragers to extract more honey than was previously possible. Hollowed-out gourds and ostrich eggs, frequently used by foragers to transport water (Howell 2010), could have been utilized to transport honey and larvae back to camp to share with dependent offspring and individuals unable to forage.[4] Routine honey consumption would have provided considerable amounts of energy, successfully supplementing meat and plant foods.

It has been suggested that the evolution of larger hominin brains, which are metabolically expensive (Aschoff et al. 1971; Holliday 1986), would have required the consumption of energy-rich foods to fuel the expansion (Aiello and Wheeler 1995; Leonard and Robertson 1994). Early members of the genus *Homo*, 1.5–2 million years ago, were the first to show signs of increased relative brain size (McHenry and Coffing 2000). This expansion coincides not only with the appearance of Oldowan tools, but also with the reduction in size of molar dentition, indicating that hominins were consuming foods that required less mechanical breakdown, i.e., chewing (Brace et al. 1987, 1991; Leonard et al. 2007). Most Paleolithic diet reconstructions emphasize the vital role that meat (Bunn 2007; Cordain et al. 2001; Eaton et al. 1998; Stanford and Bunn 2001) and/or tubers (Dominy et al. 2008; Hawkes et al. 1997; Wrangham et al. 1999) played in the shifting diet of early *Homo*. Honey, however, a food that is easy to consume and digest and is energetically dense, remains largely ignored as a component of hominin diet.

The enlarging hominin brain would have greatly benefited from the energy provided by even a modest amount of honey (Skinner 1991). Glucose plays a critical role in meeting the high metabolic requirements of neural development and function (Amiel 1994; Chugani 1998). In addition to energy, honeycomb provides small amounts of protein in the larval cells. In a highly seasonal environment such as Late Pliocene East Africa (Copeland 2007), honey and larvae may have supplemented scarce resources during the dry season. The ability to find and exploit beehives with stone tools may have been an innovation that allowed early hominins to nutritionally outcompete other species and may have been a crucial energy source to help fuel the enlarging hominin brain. To further our understanding of early hominin diet composition and the potential links between nutrition and neural expansion, we must begin to incorporate honey and larvae consumption into models of early *Homo* diet reconstruction.

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NOTES

1. The term "hominin" is a taxonomic classification used here to refer to members of the genus *Homo* and their direct ancestors, including Australopithecines.

2. Grasslands using a C_4 photosynthetic pathway (versus the more common C_3 pathway for most flowering plants) began radically changing the biosphere around 3–8 mya (Cerling 1992; Edwards et al. 2010).

3. Although Western populations are cautioned against feeding honey to infants due to the dangers of botulism (Smith et al. 2010), some rural populations routinely use honey as a weaning food (Kumar et al. 2006; Madhu et al. 2009).

4. The earliest appearance of use of a home base, or central place, dates to the Plio/Pleistocene boundary (O'Connell 1997). Early *Homo* foragers were nomadic and, as such, most likely did not store food for extended periods of time (Marlowe 2006). The preservative properties of honey, however, may have made it easier to store. It has been suggested that early hominins may have stored some foods for short periods of time as a way to combat scarcity of seasonal resources (McBrearty and Brooks 2000).

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