Journal of Human Evolution 85 (2015) 65–74

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Could plant extracts have enabled hominins to acquire honey before the control of fire?

Thomas S. Kraft[*,1], Vivek V. Venkataraman [1]

Department of Biological Sciences, Class of 1978 Life Sciences Center, Dartmouth College, Hanover, NH 03755, USA

ARTICLE INFO

Article history:
Received 20 June 2014
Accepted 19 May 2015
Available online 3 July 2015

Keywords:
Honey bee
Zoopharmacognosy
Ethnobiology
Apis

ABSTRACT

Honey is increasingly recognized as an important food item in human evolution, but it remains unclear whether extinct hominins could have overcome the formidable collective stinging defenses of honey bees during honey acquisition. The utility of smoke for this purpose is widely recognized, but little research has explored alternative methods of sting deterrence such as the use of plant secondary compounds. To consider whether hominins could have used plant extracts as a precursor or alternative to smoke, we review the ethnographic, ethnobotanical, and plant chemical ecology literature to examine how humans use plants in combination with, and independently of, smoke during honey collection. Plant secondary compounds are diverse in their physiological and behavioral effects on bees and differ fundamentally from those of smoke. Plants containing these chemicals are widespread and prove to be remarkably effective in facilitating honey collection by honey hunters and beekeepers worldwide. While smoke may be superior as a deterrent to bees, plant extracts represent a plausible precursor or alternative to the use of smoke during honey collection by hominins. Smoke is a sufficient but not necessary condition for acquiring honey in amounts exceeding those typically obtained by chimpanzees, suggesting that significant honey consumption could have predated the control of fire.

1. Introduction

The relationship between humans and honey bees is ancient and remains the subject of long-standing interest. Today, honey bees are kept in semi-domesticated conditions by beekeepers, and the honey of wild bees is harvested (i.e., honey hunting) on all continents where bees exist (Crane, 1990, 1999). Technical and industrial aspects of these practices have received detailed attention, yet the evolutionary aspects of the human-honey bee relationship have only recently been highlighted, particularly with respect to the role of honey in human dietary evolution (Crittenden, 2011; Wrangham, 2011). This topic has broad-ranging implications for understanding the evolutionary trajectory of the human lineage, in part because the emergence of human-like intelligence and life history traits is thought to be associated with specific attributes of consumed foods (discussed in Kaplan et al., 2000). Such foods should exhibit the following properties with respect to their content, and how they are harvested and distributed: 1) high quality (nutrient and calorie-dense), 2) difficult to acquire, 3) require complex tool use, 4) collected by cooperative individuals, and 5) shared among and between kin groups (Kaplan et al., 2000). Honey and associated bee brood satisfy these criteria, and recent work in evolutionary anthropology has emphasized their role in the evolution of the human diet (Crittenden, 2011; Wrangham, 2011; Venkataraman et al., 2013; Kraft et al., 2014; Marlowe et al., 2014).

While honey consumption by modern *Homo sapiens* is well documented, it is difficult to draw inferences about whether honey was a prominent food source for human ancestors such as early *Homo*. This is due in part to the virtual invisibility of honey acquisition in the archaeological and paleontological record. Other evidential approaches, however, may be used to infer honey consumption by ancient humans and possibly other members of the genus *Homo*. These include comparative studies of honey acquisition by non-human primates and observations of contemporary hunting and gathering human populations (Wrangham, 2011).

Raiding a bee hive for honey is associated with a unique set of challenges that require special morphological adaptations or cognitive capacities to overcome. Indeed, stingers laden with venom represent one of the fundamental anti-predator adaptations of honey bees to protect their hives (Schmidt, 2014). For most

* Corresponding author.
E-mail address: thomas.s.kraft@dartmouth.edu (T.S. Kraft).
[1] These authors contributed equally to the manuscript.

http://dx.doi.org/10.1016/j.jhevol.2015.05.010

vertebrate and invertebrate predators, the possibility of stings by thousands of bees represents an insurmountable barrier to honey acquisition. The stinging defenses of honey bees deter even our closest living relative, the common chimpanzee (*Pan troglodytes*), from harvesting more than miniscule amounts of honey despite the use of tools during honey collection (Boesch et al., 2009). To what extent could hominins have overcome the stinging defenses of honey bees? Research has focused on two methods to prevent bee stings to a degree that enables efficient honey harvest: 1) physical barriers and 2) smoke.

For modern humans, physical barriers include protective clothing alone since our species is primarily hairless. In other primates, the presence of body hair likely decreases the efficacy of bee stings, but only to a limited extent. For example, although chimpanzees sometimes consume *Apis* honey (Boesch and Boesch, 1990; Boesch et al., 2009; Sanz and Morgan, 2009), they typically flee quickly when stung by bees and are therefore unable to harvest great amounts. Physical barriers are effective only at avoiding stings of provoked bees, but they play no role in quelling aggression. Perhaps counter intuitively, some honey hunters eschew protective clothing and climb with only shorts or loincloths, claiming that freshly-washed bare skin is less likely to be targeted by bees (Jahai honey hunters in Peninsular Malaysia, pers. comm.). Crane (1999) notes that honey hunters may avoid clothes because bees are easily trapped in them. At any rate, the advent of clothing is relatively recent on an evolutionary timescale, having arisen ~80,000–170,000 years ago (Toups et al., 2011), which postdates the time period of interest in this article. While effective, clothing does not seem to be prerequisite to the acquisition of honey. Accordingly, in this article we do not focus on physical barriers to bee stings.

Smoke[2] is the most recognizable and common strategy of subduing bees, both by beekeepers and during honey hunting. Smoke is particularly effective because it interferes with the sensory mechanisms of bees. Specifically, smoke covers the antennae of worker bees, reducing the reception of the alarm pheromone (Visscher et al., 1995), and thereby interfering with collective defense. In addition, when confronted with smoke bees engorge themselves with honey (potentially an adaptation to facilitate escape from landscape fires), and in turn this engorgement reduces the tendency to sting (Free, 1968). As a result, the application of smoke severely reduces defensive responses and stinging behaviors (Free, 1968; Roubik, 1992; Buchmann, 2006).

The efficacy of smoke in honey collection has informed arguments about the origin of honey collection in the human lineage. Wrangham (2011) argues that honey consumption did not play a prominent role in human evolution prior to the control of fire due to the difficulty of effectively subduing stinging bees without smoke. He thus concludes that *Homo erectus* is the earliest hominid to have plausibly consumed honey in amounts exceeding that of chimpanzees[3] because it is the first species that could have controlled fire (Wrangham, 2009; Wrangham and Carmody, 2010). This argument places significant honey consumption as early as 1.8–1.9 Ma (Wrangham, 2011), although the first direct archaeological evidence for control of fire is substantially later (1.0 Ma; Berna et al., 2012).

Here we consider a third method to enable the significant harvest of honey: the use of plants. Many plants in nature produce secondary compounds that affect honey bees, and the use of plant secondary compounds during honey harvest by modern humans has been documented in several regions around the world (Crane, 1990, 1999). There has, however, been little subsequent work on this topic and its important implications for human evolutionary biology. If plant extracts alone (i.e., without smoke) can deter stinging honey bees, honey acquisition could plausibly predate the first controlled use of fire, and the current narrative regarding the role of honey in human dietary evolution may require revision.

Arriving at such a conclusion, however, requires the confirmation of at least three fundamental premises. First, hominins must have overlapped geographically and temporally with honey bees and plants containing chemicals that are successful in deterring bees. Second, hominins must have been capable of identifying specific plants that are useful during honey collection. Third, hominins must have been capable of processing and using plants in a way that renders them effective against bees.

To test theses premises, we compiled information from the literature on the range of plants and associated chemical compounds that are potentially useful in deterring[4] stinging bees. We examined the mechanisms by which these chemicals are (or are not) successful in facilitating honey collection and considered whether they differ from the physiological effects of smoke on honey bees. We then used comparative evidence from non-human primates and human foragers to explore how hominins may have harnessed the chemical attributes of plant extracts to acquire honey. We conclude by discussing the potential for plant compounds to have enabled human ancestors to acquire honey in quantities that exceed the amounts acquired by chimpanzees and rival the amounts harvested by modern hunter-gatherers.

2. Results

Table 1 contains an extensive list of plant extracts known to repel, tranquilize, pacify, or otherwise deter bees from stinging during honey harvest of wild or domesticated honey bees. This table also includes detailed information on the locations in which these plants have been documented as bee repellents, the manner in which these extracts are used, and the chemical compounds that are potentially responsible for the observed effects. Nearly all of these plants were previously identified and presented in various tables found in Crane (1990, 1999).

2.1. Plant tissues used

Species from 19 plant families have recorded uses in honey collection (Table 1). Plant tissues used during honey collection include leaves, stems, sap, and bark, but there are no reports of flowers, roots, or other underground organs being used for this purpose. Of the 35 examples presented in Table 1, 27 plants are used alone or in combination with smoke and eight plants are burned to produce more effective smoke.

2.2. Method of preparation and application

Although a few plants appear to deter bees in their natural state when worn around the neck or placed near a hive (i.e., *Hoslundia opposita* and *Shorea floribunda*), the vast majority of plants are processed for use during honey collection. In almost all cases the

[2] In this article we use the phrase 'smoke' rather than 'fire and smoke' for the sake of brevity, but we assume that the control of fire is a prerequisite to producing smoke.

[3] Hereafter we use the word "significant" to refer to amounts of honey exceeding that typically acquired by chimpanzees (see Wrangham, 2011).

[4] By deter we mean the following: making honey bees leave the comb, stay away from the comb once in flight, or prevent honey bees from stinging the honey collector. Note that according to this definition chemical 'attractants' can be considered 'deterrents.'

Table 1
Plant and fungus used during honey harvest.

Location	Population	Family	Genus	Species	Effect on bees	Method of application	Potentially active chemical compounds	Bee species affected
Democratic Republic of Congo (Svensson, 1990[,b])	Nkundu and Ntombe	Achariaceae	*Caloncoba*	*wabewesii*[a]		Direct application to skin; leaves rubbed over hands and body (Svensson, 1990[,b])		*A. mellifera*
Europe (Gerard, 1597), England (Rolfe and Rolfe, 1925)		Agaricaceae	*Calvatia*	*gigantea*	Intoxicating (Rolfe and Rolfe, 1925)	Burning to produce smoke (Rolfe and Rolfe, 1925; Cook, 1970)		*Apis mellifera unicolor* (Sirera, 1953)
Tanzania (Wood, 1983), Madagascar (Sirera, 1953)		Agaricaceae	*Calvatia*	*argentea* (listed as *Langermannia wahlbergi* in citations)	Narcotic (Wood, 1983; Mollel, 1984), toxic at high concentration (Mollel, 1984), pacifying (Mollel, 1984)	Burning to produce smoke (Wood, 1983; Mollel, 1984)	Hydrogen cyanide (Wood, 1983), Hydrogen sulfide (Mollel, 1984)	European and tropical bees (Wood, 1983), *A. mellifera*
Andaman and Nicobar islands (Dutta et al., 1983, 1985)	Onge, Jarawa, Shompen	Annonaceae	*Orophea*	*katschallica*	Repellent (Dutta et al., 1983, 1985)	Direct application to skin or application to hive; chewed leaves are smeared on skin or sprayed on hive (Dutta et al., 1983, 1985)		*A. dorsata*
Andaman islands (Awasthi, 1991)	Great Andamanese	Annonaceae	*Polyalthia*	*jenkinsii*	Repellent (Awasthi, 1991)	Direct application to skin or application to hive; chewed leaves and stem are smeared on skin and/or spit on hive (Awasthi, 1991)		*A. dorsata*
Bangladesh (Zohora, 2011)	Mouwalis (honey harvesters)	Arecaceae	*Phoenix*	*paludosa*		Burning to produce smoke (Zohora, 2011)		*A. dorsata, A. cerana*
Gabon (Coon, 1972)	Akoa	Aristolochiaceae	*Aristolochia*		Repellent	Direct application to skin; leaves are crushed into paste, mixed with sticky pulp from the fruit of an amomum tree (family Zingiberaceae), and spread over skin to prevent stings		*A. mellifera*
Tanzania (Crane, 1999)		Cannellaceae	*Warburgia*	*longimanii*[a]	Repellent			*A. mellifera*
Nepal, China (Oppitz, 1991)	Gharti	Compositae	*Artemisia*	*lactiflora*		Smoke applied to body		*A. dorsata, A. cerana*
Thailand (Crane, 1999)		Dipterocarpaceae	*Shorea*	*floribunda* (=roxburghii)	Repellent	Repels bees from vicinity; bark repels bees when placed in pots		*A. cerana*
Tanzania (Brenzinger, 1987)	Bantu (KiZigua speakers)	Euphorbiaceae	*Spirostachys*	*africana*	Narcotic	Burning to produce smoke (Brenzinger, 1987)		*A. mellifera*
Malawi (Crane, 1999), Democratic Republic of Congo (Svensson, 1990), Zimbabwe (Mukwaira, 1977)		Euphorbiaceae	*Manihot*	*esculenta*	Tranquilizer (when used to produce smoke; Mukwaira, 1977), toxic (Svensson, 1990)	Crushed up and used to block entrance (Svensson, 1990), direct application to skin (leaves rubbed on body; Crane, 1999), burning to produce smoke (Mukwaira, 1977)	Hydrocyanic acid (Svensson, 1990)	*A. mellifera*
Andaman islands (Awasthi, 1991)	Great Andamanese	Euphorbiaceae	*Antidesma*	*coriaceum*	Repellent (Awasthi, 1991)	Application to hive; chewed leaves are sprayed on hive (Awasthi, 1991)		*A. dorsata*
Zimbabwe (Mukwaira, 1977)		Fabaceae	*Vigna (Voandzeria)*	*subterranea*	Tranquilizer (Mukwaira, 1977)	Burning to produce smoke		*A. mellifera*
India (Nath et al., 1994)	Kurumbas	Fabaceae	*Albizia*	*amara*		Direct application to skin; paste made from leaves		*A. dorsata*
Zimbabwe (Mukwaira, 1977)		Lamiaceae	*Vitex*	*payos*	Tranquilizer (Mukwaira, 1977)	Burning to produce smoke		*A. mellifera*

(*continued on next page*)

Table 1 (*continued*)

Location	Population	Family	Genus	Species	Effect on bees	Method of application	Potentially active chemical compounds	Bee species affected
Mozambique (Crisp, 1939)		Lamiaceae	*Hoslundia*	*opposita*		Protection by proximity; garlands worn round neck and head prevented stinging		*A. mellifera*
"Widely reported"		Lamiaceae	*Melissa*	*officinalis*	"Preventing stings" (Howes, 1979)	Direct application to skin; leaves are rubbed on hands (Howes, 1979)	Citral, geraniol, nerol	European *A. mellifera*
India (Crane, 1999)		Lamiaceae	*Ocimum*	*sanctum (=tenuiflorum)*		Direct application to skin; leaves smeared on body		*A. cerana*
Carribean (Crane, 1990)		Malpighiaceae	*Bunchosia*	*nitida*		Direct application to skin; fresh leaves rubbed on face and arms		European *A. mellifera*
Democratic Republic of Congo	Mbuti	Maranthaceae				Burning to produce smoke (Ichikawa, 1981)		*A. mellifera*
India (Nath et al., 1994)	Kurumbas	Menispermaceae	*Cissampelos*	*pareira*	Repellent (Nath et al., 1994)	Direct application to skin; plant extract applied to skin to prevent stings (Nath et al., 1994)		*A. dorsata*
Ghana (Adjare, 1987; Yeboah-Gyan and Agyemang, 1989)		Passifloraceae	*Adenia*	*cissampeloides*	Tranquilizer	Application to hive; crushed stalks were placed near hive entrance to temporarily incapacitate bees	Cyanogenic glycosides (Quattrocchi, 2012)	*A. mellifera*
Philippines (Crane, 1999)		Piperaceae	*Piper*	*celtidiforme*		Direct application to skin; leaves rubbed on body (Crane, 1999)		*A. dorsata*
"Widely reported" (Crane, 1999)		Poaceae	*Cymbopogon*	*nardus*	"quietening"		Citral	European *A. mellifera*
India (Attri and Singh, 1978)		Verbenaceae	*Lantana*	*camara*	Repellent (Attri and Singh, 1978)	Oil from leaves used to repel bees (Attri and Singh, 1978)		*A. mellifera*
Swaziland (Crane, 1999)		Verbenaceae	*Lippia*	*javanica*	Repellent (Crane, 1999)			*A. mellifera*
Cameroon (Ross and Nicolet, 2001)	Gbaya	Verbenaceae and Euphorbiaceae	*Verbena* and *Euphorbia*		Tranquilizer; subdues the bees (Ross and Nicolet, 2001)	Leaves are mashed, inserted into nest cavity, and sealed inside		*A. mellifera*
South Andaman Island	Onge	Zingiberaceae	*Amomum*	*aculeatum*	Repellent, tranquilizer (Dutta et al., 1983)	Direct application to skin of sap from crushed stems and leaves (Dutta et al., 1983)		*A. dorsata*
Great Nicobar Island (Vasudeva Rao and Chakrabarty, 1985)	Shompens	Zingiberaceae	*Etlingera (Amomum/ Hornstedtia)*	*fenzlii*	Repellent, tranquilizer	Plant parts are chewed and sprayed on bees (Mathew et al., 2010)	Eugenol, linalool, methyl chavicol, geraniol, α-pinene, β-pinene (Mathew et al., 2010)	*A. dorsata*
Andaman	Andamanese	Zingiberaceae	*Alpinia*	*manii*	Repellent	Sap sprayed on the bees repels them by its 'obnoxious odour' or extract smeared on body (Man, 1883)		*A. dorsata*
Little Andaman	None known	Zingiberaceae	*Zingiber*	*squarrosum*	Repellent, tranquilizer (similar to *A. aculeatum*) (Dutta et al., 1983, 1985)	Same as that of *A. aculeatum*		*A. dorsata*
India		Zingiberaceae	*Zingiber*	various species		Chewed to protect face (Crane, 1999)		*A. dorsata, A. cerana*
India (Gardner, 1995)	Paliyan	Local name: eerankaiyum (wild onion)			Repellent	Chewed by honey collector (Gardner, 1995)		*A. dorsata*
India (Gardner, 1995)	Paliyan	Local name: taraku (an aromatic grass)			Repellent	Grass is bruised and held beneath comb (Gardner, 1995)		*A. cerana*

[a] Species name is cited in Crane (1999) and is probably outdated or incorrect.
[b] Reference is cited in Crane (1999) and could not be located.

plants are crushed, consistent with plant volatiles being released from vegetative parts and from sites of injury (Dudareva et al., 2004). In particular, leaves and stalks are generally crushed or chewed and mixed with saliva before they are used as repellents, tranquilizers, or narcotics (Table 1). After processing, the compounds are applied directly to the skin or placed inside the hive to kill or subdue the bees.

In some cases (e.g., *Zingiber* spp. in India; Crane, 1999) plants are chewed to protect the face. This strategy may be important because attacking bees tend to focus on the mouthparts, nose, and eyes of predators, likely by an attraction to exhaled carbon dioxide (Schmidt and Hassen, 1996), and a recent study suggests that for humans these are among the most painful areas of the body to be stung (Smith, 2014).

An alternative strategy involves burning specific plant substrates (Table 1). It is thought that burning the leaves of certain species helps to tranquilize or kill the bees, and modern beekeepers continue this practice today (sometimes additionally for the purpose of controlling pathogens or mites). However, lack of empirical data makes it difficult to discern how specific plant materials contribute to the effects of smoke as a deterrent.

2.3. Geography

Plants used during honey collection belong to speciose families and genera that occur widely in regions and habitats that are relevant to human evolution (Table 1). It is also possible that other plants from the families or genera of species known to be useful during honey collection (some of which are extremely widespread, such as *Zingiber*) may contain related chemicals and can be used for similar purposes.

2.4. Effects of chemicals on honey bee behavior

The terms used to describe the effects of plant extracts on honey bees are various (Table 1). The most common descriptions include “intoxicating,” “narcotic,” “tranquilizer,” and “repellent.” It is important to keep in mind that the precise meaning of these terms as used by the various cited authors is not always defined, probably varies between observers, and is generally qualitative and based on observational rather than experimental evidence. With this caveat in mind, some general patterns are evident. Plants used in conjunction with fire are generally described as having an intoxicating or narcotic effect, whereas crushed plants used alone serve either as a repellent, quietening agent, or tranquilizer (Table 1). Based on these qualitative descriptions, plants can affect honey bees in several capacities, being capable of exerting a similar effect to that of smoke, while also serving as a repellent.

Many plant extracts exhibit repellent and/or attractant effects on honey bees. For instance, essential oils extracted from seeds of ajwan (*Trachyspermum ammi*) and leaves of chenopodium (*Chenopodium ambrosioides*), citronella (*Cymbopogon nardus*), eucalyptus (*Eucalyptus* spp.), and lantana (*Lantana camara*) exhibit gustatory repellency to *Apis cerana indica*, with *T. ammi* and *C. ambrosioides* having the strongest effects (Kumar et al., 1986). Similarly, the essential oil of *Terminalia chebula* fruit is a dose-dependent repellent to *Apis florea* (Naik et al., 2010b), and leaf extracts from a medicinal plant in India, *Swertia densifolia*, have been shown to elicit dose-dependent repellent or attractant properties to *A. cerana indica* (Naik et al., 2005) and *A. florea* (Naik et al., 2007). *Fagara budrunga* fruit extract has also been shown to be an effective attractant of *A. cerana* (Naik et al., 2003).

In a limited number of cases the operative chemical compounds that attract or repel bees have been characterized (Detzel and Wink, 1993; Naik et al., 2008, 2010a; Sugahara et al., 2013), yielding insights into the mechanism by which plants can be used to facilitate honey harvest. Although in a few cases compounds may simply be toxic to bees (e.g., cassava leaves, see below), most relevant chemicals are likely to be semiochemicals that mimic the action of pheromones, signaling the condition of the hive or disrupting communication between bees and thus preventing colonies from mounting a collective defense response. For this reason, plant compounds resembling bee pheromones associated with attractant behavior, such as mandibular gland pheromone and chemicals in the Nasonov gland, can be used to deter bees from stinging during honey harvest. Indeed, a common stunt is for modern beekeepers to cover their bodies in queen mandibular pheromone, causing thousands of bees to converge and cover a person without becoming aggressive or stinging. Finally, while it is also possible that some compounds mask the honey bee alarm pheromone, this is unlikely because the alarm pheromones are identical across honey bee species and some plants used to deter bees are only effective against particular species (Dutta et al., 1985).

2.5. Chemical compounds

Seven plants used in honey collection listed in Table 1 are accompanied by known chemicals that change the behavior of the honey bees to facilitate honey collection. Here we focus our attention on the three instances where the plant alone is used, rather than in combination with fire.

The leaves and tubers of cassava (*Manihot esculenta*), with the exception of the tubers of some “sweet” varieties, are known to contain hydrocyanic acid (HCN) and must therefore be detoxified before consumption (Quattrocchi, 2012). Honey hunters in the Democratic Republic of Congo insert crushed cassava leaves into hives of *Apis mellifera* and block the entrances to kill the bees (Crane, 1999). Cassava leaves are also rubbed on the body to prevent stings, and cassava is otherwise described as a tranquilizer when burned to produce smoke (Mukwaira, 1977). The leaves of bitter cassava are presumably used for this purpose because they contain higher concentrations of cyanogenic glycosides, but it is not known whether honey hunters make this distinction. Leaves of cassava contain the greatest concentration of cyanogenic glycosides, containing ~5.0 g/kg of linamarin (White et al., 1998). Cyanogenesis occurs when tissue is damaged, and the resulting HCN is both highly volatile and toxic (White et al., 1998). Despite the potential for HCN to kill honey bees, however, the available evidence of use by honey hunters is anecdotal and it is not clear if such procedures result in bee mortality.

Lemon balm (*Melissa officinalis*) is used to prevent stings, and lemongrass (*C. nardus*) was described as having a quietening effect on *A. mellifera* during honey collection (Crane, 1999). Citral, geraniol, and nerol are contained in both plants and are in the terpenoid class of compounds, which generally serve as attractants to honey bees (Detzel and Wink, 1993). Likewise, *Etlingera fenzlii* contains the terpenes linalool, geraniol, α-pinene, and β-pinene (Mathew et al., 2010). Terpenoids, particularly citral, geraniol, and nerol, comprise the majority of pheromonal components emitted by the Nasanov gland of honey bees (Boch, 1962; Shearer and Boch, 1966), which is used by workers to attract nestmates to the hive and swarming locations (Williams et al., 1981; Free, 1987).

Whether the active chemical compounds in these plant materials exist in high enough concentrations to significantly modify honey bee behavior is of critical importance but has not been experimentally tested. Citral and geraniol, however, are major constituents of lemongrass and lemon balm essential oil (Burgett, 1980; Lewinsohn et al., 1998; Khanuja et al., 2005), and humans easily detect the aroma of these compounds. For example, the “lemon-like” scent of lemon balm results from concentrations of

~60% citral (Burgett, 1980; Gutierrez et al., 2008). Further, tissues of these plants have been used for centuries by beekeepers to attract swarms to empty hives (Burgett, 1980; Crane, 1999). It is thus plausible that some crushed plant materials contain sufficient terpenoids so as to exert a significant effect on honey bee behavior, but each example in Table 1 will ultimately require experimental testing before definite conclusions can be drawn.

2.6. Effectiveness of plant compounds in deterring stinging honey bees

In perhaps the best documented example of plant compounds being used to facilitate honey harvest in the absence of smoke, Cipriani (1966), Dutta et al. (1983, 1985), and Vasudeva Rao and Chakrabarty (1985) have observed the use of several Annonaceae and Zingiberaceae species during honey collection in the Andaman Islands. These plant species enable the Onge, original inhabitants of the Andaman Islands, to harvest honey efficiently and safely without the use of smoke:

> Unlike the beekeepers of the civilized world, the Onges make no attempt to protect their bare bodies while they are extracting honey. Yet they are never stung, and watching them one felt in the presence of some age-old mystery, lost by the civilized world. I watched an Onge from the ground with my field glasses as he climbed up a tree to a *dorsata* nest and saw him, as it were, blowing on the bees round about the trunk as he went up. As he approached the nest they huddled round it in a protective cloud, hiding it completely from view. Suddenly, as the Onge's face came within twenty centimetres of the boiling, humming mass, the bees seemed to shrink back as he blew on them. Not one moved to attack as he gouged out the combs with his bare hands, throwing handfuls of bees out into the air. And then the whole cloud of bees gathered into a swarm and left the tree and the nest to the interloper… In the forests of Little Andaman there are bushes of *tonjoghe* everywhere, and the Onge who is to go after the honey simply grabs a handful of the leaves and stuffs them into his mouth. With some vigorous chewing they are quickly reduced to a greenish pulp, which is smeared all over the body, particularly the hair. Another huge mouthful chewed on the way up and spat at the bees to make quite sure that they will be deterred even to the point of failing to attack the unsmeared bystanders (Cipriani, 1966: 102–103).

In Gabon, Akoa pygmies have been reported to harvest honey in a similar fashion without the use of fire:

> …the men watch the movements of the honey guide, a bird that also eats honey, and this bird leads them to the honey tree, where the best nests are located in the upper branches. Then one of the men, chosen to do the climbing, smears himself all over with a bee-repellent paste made from the juice of the crushed leaves of a species of *Aristolochus*, also used for snakebite, mixed with the sticky pulp of the fruit of an amomum tree, laying it particularly thickly over his face and hands (Coon, 1972: 163–164).

The two previous examples demonstrate that plant compounds can be highly effective at facilitating safe honey harvest. It appears that smoke would not offer a significant advantage over the use of these plants. In most of the other cases in Table 1, however, the efficacy of plant compounds used in the absence of smoke remains unknown and invites experimental testing.

3. Discussion

The inability to avoid bee stings may have prevented hominins from harvesting significant amounts of honey prior to the control of fire (Wrangham, 2011). Smoke is widely recognized to facilitate honey harvest, but the role of plant extracts for this purpose has been neglected despite many examples of use among honey hunters and beekeepers. In this article we compile evidence of humans using plant compounds to prevent bee stings during honey harvest, both in combination with smoke and independent of it (Table 1). Such evidence has implications for inferring the longevity and the nature of the predatory relationship between hominins and honey bees.

Fire would have been sufficient, but not necessary, to facilitate significant honey collection by extinct hominins. This conclusion rests on the premises presented in the introduction: first, hominins must have overlapped spatially and temporally with honey bees and plants containing chemicals that are successful in deterring bees. Second, hominins must have been capable of identifying specific plants that are useful during honey collection. Third, hominins must have been capable of processing and using plants in a way that renders them effective against bees. The available evidence provides strong support for these three premises.

3.1. Premise 1: spatial and temporal overlap

The honey bee genus, *Apis*, is thought to have originated in the early Oligocene (Engel, 1998), well before the origins of the hominin lineage in Africa. *Apis* honey is particularly important because bees in this genus produce much greater quantities of honey than other types of bees. The honey of *A. mellifera*—the only *Apis* species in Africa—has been available since ~6–8 mya and features prominently in the diets of African honey-hunters (Garnery et al., 1991; Whitfield et al., 2006; Marlowe et al., 2014). Further, these bees survive in a diversity of habitats including savanna grasslands, tropical and temperate forests, and desert (Fletcher, 1978; Crane, 1999; Kajobe and Roubik, 2006). Similarly, the plants used by humans during honey harvest are geographically widespread and phylogenetically diverse, and 13 of the examples presented occur in Africa (Table 1). Plants from at least 19 families (all of which are represented in Africa) are known to be used for this purpose, some of which are effective independent of smoke.

Compared to smoke, secondary compounds present in the vegetative tissue of plants affect honey bees through different physiological mechanisms that inhibit individual and collective defensive responses, thereby increasing the safety and/or efficiency of honey collection. Humans use plants during honey collection that have secondary compounds with (i) insecticidal and/or antifeedant properties, and/or (ii) properties that mimic pheromones used in honey bee communication. In the former case, these compounds (such as HCN) are likely to be non-specific insect repellents. Crane (1999), however, observed that some plant tissues are useful in repelling some Asian bees, but not others, indicating that the specificity of these compounds needs further research.

In the latter case, plants produce semiochemicals that mimic insect pheromones, thereby affecting insect behavior. Plant semiochemicals can stimulate insects to produce pheromones, be used as precursors for the production of insect pheromones, act synergistically with insect pheromones, and have inhibitory or repellent effects on insects (Reddy and Guerrero, 2004). For example, some plants contain components also found in the Nasanov or mandibular glands of honey bees (Crane, 1990; Sugahara et al., 2013). Nasanov and mandibular pheromones have calming or disorienting effects on honey bees that help keep collectors safe while the hive is being raided for honey. Interestingly, these secondary compounds also have dose-dependent and multi-function purposes for plants that may be co-opted in various ways. In plants, attractant and defensive (insecticidal and anti-microbial) activities can be exhibited by the same secondary compounds (Wink, 2003). In addition to disrupting insect communication, pheromones appear to act as repellents when at high concentrations (Naik et al., 1989), suggesting that even plants that produce chemicals to attract honey bees could be utilized as effective deterrents. Consistent with this notion, several plants listed in Table 1 are bee-pollinated and also used as repellents (e.g., *Vitex payos* [Mbora et al., 2008] and *Ocimum sanctum* [Kuberappa et al., 2007]).

Secondary compounds are pervasive in plants, and many are likely to have the capacity to serve as bee deterrents. For example, thousands of plant species contain endogenous cyanide-containing compounds that can release HCN, and geraniol and citral occur in the essential oils of many plants (Chen and Viljoen, 2010). If plant compounds effective in deterring bees are common, particularly within plant families that are abundant and have historically wide geographic ranges, then hominins are likely to have had repeated interactions with plant species that could be used for this purpose. In a telling example, Dutta et al. (1985: 137) discovered that *Zingiber squarrosum* is effective at tranquilizing *Apis dorsata* in the Andaman Islands "based on deductive extrapolation that other Zingiberaceae growing in the same habitat [as *Amomum aculeatum*] might also contain similarly active rock bee-tranquilising principles."

3.2. Premise 2: plant recognition

The ability to recognize and effectively utilize plant or animal material in the environment for specific purposes is not distinct to humans (Huffman, 2003). Many animals use abiotic, plant, or animal materials for medicinal purposes or to protect themselves from insects and parasites (Huffman, 2003). This process, broadly termed zoopharmacognosy (Rodriguez and Wrangham, 1993), includes the ingestion of materials with medicinal value and external application to the skin as ointment, and has been documented widely in animals, especially primates. Indeed, chimpanzees, our closest living relatives, have been repeatedly observed ingesting plant, animal, or abiotic materials for what appears to be medicinal purposes (Huffman, 1997). Such behavior requires detailed ecological knowledge given the threat posed by consumption of toxic compounds. The fact that chimpanzees are capable of effectively using plants as medicine suggests that early hominins would have been equally, if not more, capable of identifying useful plants in the environment and spreading knowledge of their utility through social interaction (Huffman, 1997).

3.3. Premise 3: processing plants

Nonhuman primates sometimes use plants materials in a way that is superficially similar to use by humans during honey collection, often involving anointment on the skin or fur. Anointing behaviors documented in non-human primates are summarized in Table 2. These behaviors are best documented in New World taxa, although orangutans provide an interesting case among the great apes (Morrogh-Bernard, 2008). Orangutans seek out the leaves of species in the genus *Commelina*, which are chewed, mixed with saliva, and lathered on the body, much in the same way that human foragers in the Andaman Islands apply Annonaceae or Zingiberaceae materials during the harvest of *A. dorsata* honey (Dutta et al., 1985; Morrogh-Bernard, 2008). In this case and many others, anointing behaviors are thought to target insects or parasites and often involve the use of carefully selected plant species following oral or manual processing (Alfaro et al., 2012).

There is limited direct evidence for the use of medicinal plants by extinct hominins because such behaviors are difficult to detect in the fossil record. Hardy et al. (2012) identified compounds in archaeological remains from Spain that indicate the use of chamomile and yarrow by Neanderthals. Although it is difficult to determine exactly how Neanderthals used these plants, their low nutritional content suggests a medicinal purpose that is congruent with modern uses of these species (Hardy et al., 2013). However, the general use of plants for self-medication in other primates provides compelling evidence for the ability of hominins to consistently identify and obtain specific plants for medicinal or protective benefit.

The above factors indicate that honey is likely to have been consistently available in time and space throughout human evolution in conjunction with plants that could be used to deter bees, and that early hominins would have been capable of identifying useful plant extracts in the environment and applying them effectively against insects. We conclude that there is substantial potential for plant materials to have been used during honey harvest by extinct hominins in a similar manner to that observed in modern humans. We emphasize that this argument does not challenge the general utility of fire in facilitating honey collection but rather adds to the documented complexity of primate honey-collecting behavior. We concur with Wrangham (2011) that if *H. erectus* were the first hominin to control fire, then it probably harvested honey more effectively than its progenitors. The use of fire benefits from its universal availability, effectiveness, and simplicity compared to detailed ethnobotanical knowledge. The depiction in Zimbabwean rock paintings from ~8000 BC of smoke being used during honey collection (Crane, 1999) attests to the antiquity and effectiveness of this method. However, the specificity of plants chosen as torches during honey collection emphasizes the importance of plant secondary compounds, even when used in association with smoke (Table 1; Crane, 1990, 1999).

With the limited data available it is difficult to discern the conditions under which plant compounds are favored during honey collection, sometimes in place of fire. Cipriani (1966) suggests that the use of plants during honey collection in the Andaman Islands might have been prominent because the Andamanese lacked the ability to make fire (although they used fire from lightning strikes opportunistically). Although Cipriani's claim that the Andamanese lacked the ability to make fire may be exaggerated (cf. Gott, 2002), fire-making is undoubtedly more difficult in moist tropical forest conditions. Such circumstances increase the time and effort required to utilize smoke during honey harvest and thus make plant materials a more attractive alternative. In the other cases presented in Table 1, however, lack of fire is unlikely to be a contributing factor. Instead, plants probably enhance the safety of honey collectors even if smoke is simultaneously employed to pacify bees.

3.4. Future directions

Further investigation of hominin honey harvesting capability in the absence of smoke can be advanced in several ways. First, although anecdotal evidence suggests that plant compounds can be extremely effective (Dutta et al., 1983, 1985), the efficacy of specific plant compounds at preventing bee stings has not been evaluated quantitatively in comparison to smoke. Simple aggression experiments following the research design of Free (1961), Seeley et al. (1982), or Wray et al. (2011) should be conducted to elucidate the relative effectiveness of the plants identified in Table 1, associated chemical compounds in isolation, and smoke. For example, test substances can be applied to dummy targets presented at

Table 2
Self-anointment behaviors in nonhuman primates.

Species	Materials used	Method of application	Putative purpose	Reference(s)
Aotus spp.	Plants: *Piper marginatum* extract, onion, garlic, chives. Animals: millipede (*Anadenobolus monilicornus*), millipede-produced benzoquinones	Plants: Manual application to body Animals: Manual application to body	Protection against insects; social function	(Zito et al., 2003; Jefferson et al., 2014)
Ateles geoffroyi	Plants: *Apium graveolens, Brongniartia alamosana, Cecropia obtusifolia, Citrus aurantifolia, Zanthoxylum procerum, Z. belizense*	Leaves chewed, mixture with saliva lathered manually on body	Social communication	(Campbell, 2000; Laska et al., 2007)
Callicebus sp. (captive)	Plants: onion. Other: ice cubes	Rubbed over body with saliva		(Fragaszy et al., 2004)
Cebus albifrons	Plants: *Alibertia curviflora* fruit, *Citrus* spp., *Genipa americana* fruit, hot peppers, onion, *Pentaclethra macroloba* seed pods, *Phytelephaspalm* flowers. Other: bleach, cigarettes, cologne, DEET repellent, liquid soap, powdered detergent, wet or dry mud	Pod is broken apart and the inside is rubbed against the body (*Pentaclethra macroloba* seed pods). Other substances rubbed directly onto body.	Antiseptic; insect repellent; antifungal	(Baker, 1999; Field, 2007; Alfaro et al., 2012)
Cebus apella	Animals: Carpenter ant (*Camponotus rufipes*), millipede (*Orthoporus dorsovittatus*)-produced benzoquinones	Animals: Ants or millipedes rubbed into fur, sometimes mixed with urine during application	Protection against ectoparasites and insects	(Weldon et al., 2003; Verderane et al., 2007)
Cebus capucinus	Plants: *Annona* sp., *Caesalpinia eropstacjus*, *Citrus* sp., *Clematis* stems, unripe *Capsicum, Dieffenbachia* sp., *Eugenia nesiotica*, *Eugenia salamanensis* fruit, *Gliricidia sepium, Hymenaea courbaril* sap, *Jacquinia pungens* fruit, *Laetia thamnia*, *Miconia argentea*, mint, *Pithecellobium saman* sap, *Piper marginatum* leaves and *Piper tuberculatum* immature fruits, *Protium* sp., *Sloanea* seed pods, *Sloanea terniflora* fruit, *Tetrathylacium johansenii*, *Trichilia americana, Virola surinamensis*. Animals: Stink bug, ant (*Camponotus sericeiventris*), carpenter ant, millipede, millipede (*Orthoporus dorsovittatus*)-produced benzoquinonescaterpillars. Other: Mud, water from *Hymenaea courbaril*, water from *Pithecellobium samans*	Plants: Manual application to body Animals: Manual application to body	Protection against ectoparasites, insects; social facilitation; by-product of foraging; antibacterial; antifungal	(Oppenheimer, 1968; Buckley, 1983; Longino, 1984; Baker, 1996; DeJoseph et al., 2002; Weldon et al., 2003; O'Malley and Fedigan, 2005; Perry, 2008; Alfaro et al., 2012)
Cebus olivaceus	Animals: Millipede (*Orthoporus dorsovittatus*)	Millipede is taken in mouth and then rubbed vigorously on body	Protection against insects	(Valderrama et al., 2000)
Eulemur macaco	Animals: Millipedes (*Charactopygus* sp.)	Millipede is chewed and rubbed vigorously on body	Protection against ectoparasites, insects; treatment of skin disease; enhancement of olfactory communication; production of an agreeable sensation on skin	(Birkinshaw, 1999)
Pongo pygmaeus	Plants: *Commelina* sp.	Leaves chewed, mixture with saliva lathered directly on body	Anti-bacterial; anti-inflammatory	(Morrogh-Bernard, 2008)
Saimiri sp. (captive)	Plants: onion. Other: ice cubes	Rubbed over body with saliva		(Fragaszy et al., 2004)
Sapajus apella	Plants: rotten bamboo leaves			(Leca et al., 2007)
Sapajus libidinosus	Animals: Ants (Formicidae), stink bugs (Nezara viridula), caterpillars, crickets, millipedes, praying mantis. Other: Quartz powder	Rubbed on body, sometimes incorporated urine washing		(Mannu and Ottoni, 2009; Alfaro et al., 2012)
Sapajus nigritus	Animals: Ants, spiny green caterpillars wasps	Caterpillar rolled on branch and then rubbed on fur		(Alfaro et al., 2012)

aggravated hives, and the number of stings received by the target or the amount of guard bees mobilized can be quantified.

Second, it would be useful to know whether any non-human primates employ plant compounds during honey harvest. Chimpanzees use plant-derived tools during honey collection (Brewer and McGrew, 1990; Kajobe and Roubik, 2006; Boesch et al., 2009; Sanz and Morgan, 2009). The suite of complex tools used by chimpanzees sometimes includes branches of specific species with attached leaves or chewed bark (Sanz and Morgan, 2009), although in the vast majority of cases leaves are stripped and the branch is used as a mechanical tool (Boesch et al., 2009). It would be useful to consider the possibility that plants used during honey collection by non-human primates could be selected for chemical properties that help deter stinging bees (or even plant tissue attracting ants in the case of termite-fishing), and future studies should ideally address the selectivity and experimental efficacy of plant species used as honey tools.

Finally, it is important that anthropologists and ethnobiologists continue to document the diversity of plants used to deter bees by beekeepers and honey hunters around the world. The use of plants during honey collection is undoubtedly more widespread than the available literature would indicate, and Table 1 is likely a small and unrepresentative sample. Following the tradition of Eva Crane (Crane, 1990, 1999), documenting these practices is not only timely for paleoanthropology but also critically important for preserving cultural heritage as traditional beekeeping and honey hunting techniques are rapidly being replaced by standardized industrial practices.

4. Conclusions

As evidence mounts for a role of honey in the evolution of the human diet (Crittenden, 2011; Wrangham, 2011; Kraft et al., 2014; Marlowe et al., 2014), it is important to consider the antiquity of what we have referred to as significant honey collection. Many researchers believe that the control of fire is necessary for significant honey collection. Here we present evidence demonstrating that plant extracts can effectively facilitate honey collection and that extinct hominins were likely capable of identifying, processing, and applying plant materials for this purpose. We conclude that significant honey consumption is not constrained by, and may therefore predate, the control of fire.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgments

We thank Richard Wrangham, Nathaniel Dominy, Edmond Dounias, Nicolas Cesard, and Thomas Seeley for helpful discussions during the writing of this article. T.S.K. and V.V.V. are supported by National Science Foundation Graduate Research Fellowships.

References

Adjare, S., 1987. Ghana. IBRA Newsl. 11, p. 7.
Alfaro, J.W.L., Matthews, L., Boyette, A.H., Macfarlan, S.J., Phillips, K.A., Falótico, T., Ottoni, E., Verderane, M., Izar, P., Schulte, M., 2012. Anointing variation across wild capuchin populations: a review of material preferences, bout frequency and anointing sociality in *Cebus* and *Sapajus*. Am. J. Primatol. 74, 299–314.
Attri, B., Singh, R., 1978. A note on the biological activity of the oil of *Lantana camara* L. Indian J. Entomol. 39, 384–385.
Awasthi, A.K., 1991. Ethnobotanical studies of the negrito islanders of Andaman Islands, India—the Great Andamanese. Econ. Bot. 45, 274–280.
Baker, M., 1996. Fur rubbing: use of medicinal plants by capuchin monkeys (*Cebus capucinus*). Am. J. Primatol. 38, 263–270.
Baker, M., 1999. Fur rubbing as evidence for medicinal plant use by capuchin monkeys (*Cebus capucinus*): ecological, social, and cognitive aspects of the behavior. Ph.D. Dissertation, University of California, Riverside.
Berna, F., Goldberg, P., Horwitz, L.K., Brink, J., Holt, S., Bamford, M., Chazan, M., 2012. Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province. South Africa. Proc. Natl. Acad. Sci. USA 109, E1215–E1220.
Birkinshaw, C.R., 1999. Use of millipedes by black lemurs to anoint their bodies. Folia Primatol. 70, 170–171.
Boch, R., 1962. Identification of geraniol as the active component in the Nassanoff pheromone of the honey bee. Nature 194, 704–706.
Boesch, C., Boesch, H., 1990. Tool use and tool making in wild chimpanzees. Folia Primatol. 54, 86–99.
Boesch, C., Head, J., Robbins, M.M., 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park. Gabon. J. Hum. Evol. 56, 560–569.
Brenzinger, M., 1987. East African beekeeping vocabularies: kiZigua. Afrikanistische Arbeitspapiere 9, 113–123.
Brewer, S.M., McGrew, W.C., 1990. Chimpanzee use of a tool-set to get honey. Folia Primatol. 54, 100–104.
Buchmann, S.L., 2006. Letters from the Hive: An Intimate History of Bees, Honey, and Humankind. Random House Inc., New York.
Buckley, J.S., 1983. The feeding behavior, social behavior, and ecology of the white-faced monkey *Cebus capucinus* at Trujillo, Northern Honduras, Central America. Ph.D. Dissertation, University of Texas at Austin.
Burgett, M., 1980. The use of lemon balm (*Melissa officinalis*) for attracting honeybee swarms. Bee World 61, 44–46.
Campbell, C.J., 2000. Fur rubbing behavior in free-ranging black-handed spider monkeys (*Ateles geoffroyi*) in Panama. Am. J. Primatol 51, 205–208.
Chen, W., Viljoen, A.M., 2010. Geraniol—a review of a commercially important fragrance material. S. Afr. J. Bot. 76, 643–651.
Cipriani, L., 1966. The Andaman Islanders. Frederick A. Praeger, New York.
Cook, V.A., 1970. Puff ball control of bees. New Zeal. J. Agric. 120, 72–73.
Coon, C.S., 1972. The Hunting Peoples. Jonathan Cape, London.
Crane, E., 1990. Bees and Beekeeping: Science, Practice and World Resources. Cornell University Press, Ithaca.
Crane, E., 1999. The World History of Beekeeping and Honey Hunting. Routledge, New York.
Crisp, F., 1939. A bee repellent plant. S. Afr. Bee J. 13, 112.
Crittenden, A.N., 2011. The importance of honey consumption in human evolution. Food Foodways 19, 257–273.
DeJoseph, M., Taylor, R.S.L., Baker, M., Aregullin, M., 2002. Fur-rubbing behavior of capuchin monkeys. J. Am. Acad. Dermatol. 46, 924–925.
Detzel, A., Wink, M., 1993. Attraction, deterrence or intoxication of bees (*Apis mellifera*) by plant allelochemicals. Chemoecology 4, 8–18.
Dudareva, N., Pichersky, E., Gershenzon, J., 2004. Biochemistry of plant volatiles. Plant Physiol. 135, 1893–1902.
Dutta, T.R., Ahmed, R., Abbas, S.R., 1983. Discovery of a plant in the Andaman islands that tranquilizes *Apis dorsata*. Bee World 64, 158–163.
Dutta, T., Ahmed, R., Abbas, S., Vasudeva Rao, M., 1985. Plants used by Andaman aborigines in gathering rock-bee honey. Econ. Bot. 39, 130–138.
Engel, M., 1998. Fossil honey bees and evolution in the genus *Apis* (Hymenoptera: Apidae). Apidologie 29, 265–281.
Field, M., 2007. If you give a monkey an onion: an introduction to fur rubbing in human-commensal white-fronted capuchin monkeys (*Cebus albifrons*). Am. J. Phys. Anthropol. 44, 108.
Fletcher, D.J.C., 1978. The African bee, *Apis mellifera adansonii*, in Africa. A. Rev. Entomol. 23, 151–171.
Fragaszy, D.M., Visalberghi, E., Fedigan, L., 2004. The Complete Capuchin: The Biology of the Genus *Cebus*. Cambridge University Press, New York.
Free, J.B., 1961. The stimuli releasing the stinging response of honeybees. Anim. Behav. 9, 193–196.
Free, J.B., 1968. Engorging of honey by worker honeybees when their colony is smoked. J. Apic Res. 7, 135–138.
Free, J.B., 1987. Pheromones of Social Bees. Chapman and Hall, London.
Gardner, P., 1995. Illness and response among South Indian foragers. Med. Anthropol 16, 119–139.
Garnery, L., Vautrin, D., Cornuet, J., Solignac, M., 1991. Phylogenetic relationships in the genus *Apis* inferred from mitochondrial DNA sequence data. Apidologie 22, 87–92.
Gerard, J., 1597. The Herball or Generall Historie of Plantes. I. Norton, London.
Gott, B., 2002. Fire-making in Tasmania: absence of evidence is not evidence of absence. Curr. Anthropol. 43, 650–656.
Gutierrez, J., Barry-Ryan, C., Bourke, P., 2008. The antimicrobial efficacy of plant essential oil combinations and interactions with food ingredients. Int. J. Food Microbiol. 124, 91–97.
Hardy, K., Buckley, S., Collins, M.J., Estalrrich, A., Brothwell, D., Copeland, L., García-Tabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Cortés, A., 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, 873–877.
Howes, N.F., 1979. Plants and Beekeeping. Faber, London.
Huffman, M.A., 1997. Current evidence for self-medication in primates: a multidisciplinary perspective. Yrbk. Phys. Anthropol. 40, 171–200.

Huffman, M.A., 2003. Animal self-medication and ethno-medicine: exploration and exploitation of the medicinal properties of plants. Proc. Nutr. Soc. 62, 371–381.

Ichikawa, M., 1981. Ecological and sociological importance of honey to the Mbuti net hunters, Eastern Zaire. Afr. Study Monogr. 1, 55–68.

Jefferson, J.P., Tapanes, E., Evans, S., 2014. Owl monkeys (*Aotus* spp.) perform self- and social anointing in captivity. Folia Primatol. 85, 119–134.

Kajobe, R., Roubik, D.W., 2006. Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve. Biotropica 38, 210–218.

Kaplan, H., Hill, K., Lancaster, J., Hurtado, A.M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol. Anthropol. 9, 156–185.

Khanuja, S., Shasany, A.K., Pawar, A., Lal, R.K., Darokar, M.P., Naqvi, A.A., Rajkumar, S., Sundaresan, V., Lal, N., Kumar, S., 2005. Essential oil constituents and RAPD markers to establish species relationship in *Cymobopogon* Spreng. (Poaceae). Biochem. Syst. Ecol. 33, 171–186.

Kraft, T.S., Venkataraman, V.V., Dominy, N.J., 2014. A natural history of human tree climbing. J. Hum. Evol. 71, 105–118.

Kuberappa, G.C., Shilpa, P., Vishwas, A.B., Vasundhara, M., 2007. Insect pollinators abundance and their activity in vishnu tulasi (*Ocimum sanctum* L.). Biomed 2, 260–264.

Kumar, J., Patyal, S.K., Mishra, R.C., 1986. Evaluation of some essential oils as repellents to the Indian honeybee *Apis cerana indica* 1. Gustatory repellency and toxicity. J. Apic Res. 25, 256–261.

Laska, M., Bauer, V., Salazar, L.T.H., 2007. Self-anointing behavior in free-ranging spider monkeys (*Ateles geoffroyi*) in Mexico. Primates 48, 160–163.

Leca, J.-B., Gunst, N., Petit, O., 2007. Social aspects of fur-rubbing in *Cebus capucinus* and *C. apella*. Int. J. Primatol. 28, 801–817.

Lewinsohn, E., Dudai, N., Tadmor, Y., Katzir, I., Ravid, U., Putievsky, E., Joel, D.M., 1998. Histochemical localization of citral accumulation in lemongrass leaves (*Cymbopogon citratus* [DC.] Stapf., Poaceae). Annals Bot. 81, 35–39.

Longino, J.T., 1984. True anting by the capuchin, *Cebus capucinus*. Primates 25, 243–245.

Man, E., 1883. The Aboriginal Inhabitants of the Andaman Islands. Mittal Publications, New Delhi.

Mannu, M., Ottoni, E.B., 2009. The enhanced tool-kit of two groups of wild bearded capuchin monkeys in the Caatinga: tool making, associative use, and secondary tools. Am. J. Primatol. 71, 242–251.

Marlowe, F.W., Berbesque, J.C., Wood, B., Crittenden, A., Porter, C., Mabulla, A., 2014. Honey, Hadza, hunter-gatherers, and human evolution. J. Hum. Evol. 71, 119–128.

Mathew, S.P., Radha, R.K., Krishnan, P.N., Seeni, S., 2010. Phytogeography of the Andaman-Nicobar Islands with special reference to *Hornstedtia fenzlii* (Kurz) K. Schum. Curr. Sci. 98, 905–907.

Mbora, A., Jamnadass, R., Lillesø, J.P., 2008. Growing High Priority Fruits and Nuts in Kenya: Uses and Management. World Agroforestry Centre, Nairobi.

Mollel, L., 1984. The use of puffballs *Langermannia wahlbergi* as bee repellents. IBRA Newslett. 12, 14.

Morrogh-Bernard, H.C., 2008. Fur-rubbing as a form of self-medication in *Pongo pygmaeus*. Int. J. Primatol. 29, 1059–1064.

Mukwaira, B., 1977. Traditional and transitional beekeeping in Rhodesia. In: Fletcher, D.J.C. (Ed.), African Bees: Taxonomy, Biology and Economic Use. Apimondia, Pretoria, pp. 103–106.

Naik, D.G., Kapadi, A.H., Singh, M.K., Suryanarayana, M.C., Kshirsagar, K.K., 1989. Lure development for Indian honey bees *Apis cerana indica* Fabr. Indian Bee J. 51, 47–50.

Naik, D., Banhatti, P., Chawda, S., Thomas, D., 2003. *Fagara bundruna* fruit extract as an attractant for *Apis cerana*. J. Apic Res. 42, 48–49.

Naik, D., Dandge, C., Puntambekar, H., Patil, T., 2005. Attractant and repellent properties of *Swertia densifolia* leaf extract towards *Apis cerana indica*. J. Apic Res. 44, 116–118.

Naik, D., Dandge, C., Puntambekar, H., 2007. *Swertia densifolia* leaf extract as a dose-dependant attractant or repellent for *Apis florea*. J. Apic Res. 46, 15–18.

Naik, D., Dandge, C., Puntambekar, H., Deshpande, P., 2008. Chemical examination of *Swertia densifolia* leaf essential oil and its repellent activity towards *Apis cerana indica* F. J. Apic Res. 47, 63–67.

Naik, D., Dandge, C., Deshpande, P., 2010a. "Pheromone-like" properties of de-oiled leaf extract of *Swertia densifolia* towards *Apis cerana* F. J. Apic Res. 49, 149–153.

Naik, D., Puntambekar, H., Anantpure, P., 2010b. Essential oil of *Terminalia chebula* fruits as a repellent for the Indian honeybee *Apis florea*. Chem. Biodivers. 7, 1303–1310.

Nath, S., John, M., Roy, P., 1994. Honeyhunters and beekeepers of Tamil Nadu: climbing through a period of change. Newsletter: Forest, Trees, and People 29.

O'Malley, R.C., Fedigan, L., 2005. Variability in food-processing behavior among white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am. J. Phys. Anthropol. 128, 63–73.

Oppenheimer, J.R., 1968. Behavior and ecology of the white-faced monkey, *Cebus capucinus*, on Barro Colorado Island, CZ. Ph.D. Dissertation, University of Illinois at Urbana-Champaign.

Oppitz, M., 1991. Beekeeping and the hunt for wild honey among the Magar of Nepal. Bee World 72, 165–169.

Perry, S., 2008. Manipulative Monkeys: The Capuchins of Lomas Barbudal. Harvard University Press, Cambridge.

Quattrocchi, U., 2012. CRC World Dictionary of Medicinal and Poisonous Plants: Common Names, Scientific Names, Eponyms, Synonyms, and Etymology. CRC Press, London.

Reddy, G.V.P., Guerrero, A., 2004. Interactions of insect pheromones and plant semiochemicals. Trends Plant Sci. 9, 253–261.

Rodriguez, E., Wrangham, R., 1993. Zoopharmacognosy: the use of medicinal plants by animals. In: Downum, K., Romeo, J., Stafford, H. (Eds.), Phytochemical Potential of Tropical Plants. Springer, New York, pp. 89–105.

Rolfe, R.T., Rolfe, F.W., 1925. The Romance of the Fungus World. Chapman and Hall, Limited, London.

Ross, J., Nicolet, G., 2001. Suiting up for the honey wars. Smithsonian 32, 78–83.

Roubik, D.W., 1992. Ecology and Natural History of Tropical Bees. Cambridge University Press, Cambridge.

Sanz, C.M., Morgan, D.B., 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. Int. J. Primatol. 30, 411–427.

Schmidt, J.O., 2014. Evolutionary responses of solitary and social Hymenoptera to predation by primates and overwhelmingly powerful vertebrate predators. J. Hum. Evol. 71, 12–19.

Schmidt, J.O., Hassen, L.V.B., 1996. When Africanized bees attack: what you and your clients should know. Vet. Med. 91, 923–928.

Seeley, T.D., Seeley, R.H., Akratanakul, P., 1982. Colony defense strategies of the honeybees in Thailand. Ecol. Monogr. 52, 43–63.

Shearer, D.A., Boch, R., 1966. Citral in the Nassanoff pheromone of the honey bee. J. Insect Physiol. 12, 1513–1521.

Sirera, J., 1953. Chasse et Capture des Abeilles dans les Cinq Parties du Monde. Author, Aude.

Smith, M.L., 2014. Honey bee sting pain index by body location. PeerJ 2, e338.

Sugahara, M., Izutsu, K., Nishimura, Y., Sakamoto, F., 2013. Oriental orchid (*Cymbidium floribundum*) attracts the Japanese honeybee (*Apis cerana japonica*) with a mixture of 3-hydroxyoctanoic acid and 10-hydroxy-(E)-2-decenoic acid. Zool. Sci. 30, 99–104.

Svensson, B., 1990. Des abeilles mellifères au Bandundu du Nord, Zaire. RS Taurus, Motala, Sweden.

Toups, M.A., Kitchen, A., Light, J.E., Reed, D.L., 2011. Origin of clothing lice indicates early clothing use by anatomically modern humans in Africa. Mol. Biol. Evol. 28, 29–32.

Valderrama, X., Robinson, J.G., Attygalle, A.B., Eisner, T., 2000. Seasonal anointment with millipedes in a wild primate: a chemical defense against insects? J. Chem. Ecol. 26, 2781–2790.

Vasudeva Rao, M.K., Chakrabarty, T., 1985. Two more plants used in gathering honey. J. Econ. Taxon. Bot. 7, 643–644.

Venkataraman, V.V., Kraft, T.S., Dominy, N.J., 2013. Tree climbing and human evolution. Proc. Natl. Acad. Sci. USA 110, 1237–1242.

Verderane, M.P., Falótico, T., Resende, B.D., Labruna, M.B., Izar, P., Ottoni, E.B., 2007. Anting in a semifree-ranging group of *Cebus apella*. Int. J. Primatol. 28, 47–53.

Visscher, P.K., Vetter, R.S., Robinson, G.E., 1995. Alarm pheromone perception in honey bees is decreased by smoke (Hymenoptera: Apidae). J. Insect Behav. 8, 11–18.

Weldon, P.J., Aldrich, J.R., Klun, J.A., Oliver, J.E., Debboun, M., 2003. Benzoquinones from millipedes deter mosquitoes and elicit self-anointing in capuchin monkeys (*Cebus* spp.). Naturwissenschaften 90, 301–304.

White, W.L.B., Arias-Garzon, D.I., McMahon, J.M., Sayre, R.T., 1998. Cyanogenesis in cassava: the role of hydroxynitrile lyase in root cyanide production. Plant Physiol. 116, 1219–1225.

Whitfield, C.W., Behura, S.K., Berlocher, S.H., Clark, A.G., Johnston, J.S., Sheppard, W.S., Smith, D.R., Suarez, A.V., Weaver, D., Tsutsui, N.D., 2006. Thrice out of Africa: ancient and recent expansions of the honey bee, *Apis mellifera*. Science 314, 642–645.

Williams, I.H., Pickett, J.A., Martin, A.P., 1981. The Nasonov pheromone of the honeybee *Apis mellifera* L. (Hymenoptera, Apidae). Part II. Bioassay of the components using foragers. J. Chem. Ecol. 7, 225–237.

Wink, M., 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. Phytochemistry 64, 3–19.

Wood, W.F., 1983. Anaesthesia of honeybees by smoke from the pyrolysis of puffballs and keratin. J. Apic Res. 22, 107–110.

Wrangham, R.W., 2009. Catching Fire: How Cooking Made us Human. Basic Books, New York.

Wrangham, R.W., 2011. Honey and fire in human evolution. In: Pilbeam, D., Sept, J. (Eds.), Casting the Net Wide: Papers in Honor of Glynn Isaac and His Approach to Human Origins Research. Oxbow Books, Oxford.

Wrangham, R.W., Carmody, R., 2010. Human adaptation to the control of fire. Evol. Anthropol. 19, 187–199.

Wray, M.K., Mattila, H.R., Seeley, T.D., 2011. Collective personalities in honeybee colonies are linked to colony fitness. Anim Behav. 81, 559–568.

Yeboah-Gyan, K., Agyemang, O., 1989. Extracts of ahomafufuo (a species of *Adenia*, Passifloraceae) as anaesthetic for tropical African honeybees (*Apis mellifera*). Proc. 4th Int. Conf. Apic. Trop. Climates, pp. 37–39.

Zito, M., Evans, S., Weldon, P.J., 2003. Owl monkeys (*Aotus* spp.) self-anoint with plants and millipedes. Folia Primatol. 74, 159–161.

Zohora, F.T., 2011. Non-timber forest products and livelihoods in the Sunderbans. In: Livelihoods, Rural, Landscapes, Protected (Eds.), Co-Management in the Wetlands and Forests of Bangladesh. Nishorgo Network, Dhaka, pp. 99–117.