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

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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

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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.'