



Original Article

Mutualism and manipulation in Hadza–honeyguide interactions

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ABSTRACT

We investigated the ecology and evolution of interspecific cooperation between the Greater Honeyguide bird, *Indicator indicator*, and human hunter-gatherers, the Hadza of northern Tanzania. We found that honeyguides increased the Hadza's rate of finding bee nests by 560%, and that the birds led men to significantly higher yielding nests than those found without honeyguides. We estimate that 8–10% of the Hadza's total diet was acquired with the help of honeyguides. Contrary to most depictions of the human-honeyguide relationship, the Hadza did not actively repay honeyguides, but instead, hid, buried, and burned honeycomb, with the intent of keeping the bird hungry and thus more likely to guide again. Such manipulative behavior attests to the importance of social intelligence in hunter-gatherer foraging strategies. We present an evolutionary model for human-honeyguide interactions guided by the behavioral ecology of bees, non-human primates, and hunter-gatherers.

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1. Introduction

When searching their woodlands for nests of honey bees, Hadza hunter-gatherers are often helped by the Greater Honeyguide (*Indicator indicator*, hereafter 'honeyguide'), a bird that flies ahead of them, leading them to nests of the honey bee, *Apis mellifera*. In this article, we 1) describe how Hadza and honeyguides interacted; 2) test whether honeyguides changed the Hadza's efficiency at finding honey; 3) estimate the fraction of the Hadza's diet that was acquired with honeyguides' help; 4) examine how and why the Hadza manipulate honeyguides; 5) discuss the evolution of this relationship.

These research questions arise as part of our ongoing studies of Hadza behavioral ecology (Marlowe, 2003, 2010; Marlowe & Berbesque, 2009; Pontzer et al., 2012; Raichlen et al., 2014; Wood, 2006; Wood & Marlowe, 2013). Here, we are guided by theories of the evolution and maintenance of social foraging strategies, using rates of energy capture as a proxy variable for fitness benefits (Smith & Winterhalder, 1992; Winterhalder, 1996). We define *mutualism* in the standard manner as an interaction that provides net benefits to both parties, and *commensalism* as an interaction which provides net benefits to one party and does no harm to the other (Boucher, James, & Keeler, 1982; Connor, 1995). We use the term *manipulation* here to refer to an act by partner A that causes partner B to alter its behavior in a way that is beneficial to A and marginally costly to B.

Archaeologists have paid special attention to the role of mutualistic interactions between humans and other species, largely in order to understand the processes of plant and animal domestication (Rindos, 1980). One goal of this paper is to provide a case study of cooperation between humans and a wild animal partner. We hope this study will help foster an appreciation for the diverse ways in which people like the Hadza engage and influence their ecosystems, embedded in a full suite of species interactions including but not restricted to predation.

1.1. Hadza, honey, and honeyguides

The Hadza are an ethnic group that has traditionally subsisted from hunting and gathering who live in northern Tanzania near Lake Eyasi (latitude −3.3 to 4.0; longitude 34.6–35.6; elevation 1200–1600 m). Today there exist approximately 1200 speakers of the Hadza language, among whom about 250 continue to hunt and gather with traditional technologies for approximately 95% of their total diet. More ethnographic details and information about Hadza subsistence can be found in other publications (Marlowe, 2010; Wood & Marlowe, 2013).

In cultures around the world, honey is highly prized as food and medicine, and there is no known culture with a taboo prohibiting its consumption¹. Honey forms an important part of the diet of many

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¹ Based on a search of 258 cultures coded in eHRAF World Cultures. 5 cultures (2%) have transient prohibitions against consumption of some types of honey by a subset of the population during political gatherings, initiation rites, religious gatherings, and crop plantings.

foraging populations in tropical and temperate zones with adequate precipitation (Marlowe et al., 2014). With its warm temperatures, adequate rainfall, wide diversity of flowering plants, and many trees suitable for bee nests, the Hadza's environment is very favorable to bee life and honey production. Unlike their pastoralist or agriculturalist neighbors, the Hadza do not construct beehives, but there are standing trees in Hadza country that individuals harvest honey from over many years, even generations. After the Hadza cut open a tree to access a bee nest, they subsequently place stones into the opening to encourage bees to re-occupy the same tree. In this way, Hadza honey-hunters contribute both to the destruction and construction of bee nests.

The Hadza recognize 7 species of honey producing bees, six of which are small stingless bees. The large stinging *Apis mellifera* ('awawa' to the Hadza) is by far the most important species in terms of honey production, which reaches its peak during the late wet season (March–May), in synch with peak plant flowering and nectar production. During this time, ~20% of the food that Hadza bring back to camp, by weight, is honey (Marlowe & Berbesque, 2009). Based on foods brought into Hadza camps, Marlowe et al. (2014) estimate that 15% of the total yearly calories that Hadza consume in camp is honey.

Apis mellifera nests are often located high in baobab trees, and can therefore be difficult to spot and access. Falling from trees while harvesting honey is a major source of injury and death for Hadza men (Bennett, Barnicot, Woodburn, Pereira, & Henderson, 1973; Blurton Jones & Marlowe, 2002). *A. mellifera* typically mount a fearsome defense of their colonies, but with the use of smoke, and a high tolerance for bee stings, Hadza men climb into trees and raid their nests. Women sometimes accompany men on honey hunting trips, helping to search for bee nests, light and tend fires, and process the honey that men extract. Women will also occasionally chop open the nests of small stingless bees (*Meliponini*) and harvest their honey, but long-term data indicate that men acquire the vast majority of all honey (Marlowe, 2010; Marlowe et al., 2014). In all our observations, men have carried out the dangerous work of climbing trees, disturbing *A. mellifera* colonies, and extracting honey from the colony's nest.

Interviews with Hadza indicate that both men and women prefer honey over all other food types (Berbesque & Marlowe, 2009). While honey collecting is most profitable during the wet season, men consistently forage for honey throughout the year, and it is normal for men to carry, along with their bow and arrows, an ax and a container for carrying honey. When men return to camp with honey, there is a high public demand for sharing, but men often place all the honey they have brought back to camp directly into their households, or hand it all to their wives. Quantitative analysis of sharing patterns by married men shows that they preferentially share with their wives, children, and relatives living in other households (Wood & Marlowe, 2013).

Cooperation between African honey-hunters and honeyguide birds caught the attention of early European explorers of East and Southern Africa, who published accounts of honeyguides leading people to nests of honey bees (Dos Santos, 1891; Spaarman, 1777). In modern times, this intriguing relationship has been featured in textbooks, trade books, magazines, and films to illustrate interspecific cooperation (Bernard & Bennett, 1996; Danchin, Giraldeau, & Cézilly, 2008; Flannery, 2011; Friedmann, 1954, 1955; Grunton, 1990; Orrians, 2014; Queeny, 1952; Sayre & Schindler, 2000; Stone, 2011). Honeyguides are the only wild animal known to actively guide people to sources of food. A somewhat analogous case of interspecific cooperation has been reported in Brazil and Myanmar, where wild dolphins (*Transiops truncatus* and *Orcaella brevirostris*, respectively) drive fish towards fishermen's nets, a joint foraging tactic that seems to mutually benefit both parties (Pryor & Lindbergh, 1990; Zappes, Andriolo, Simões-Lopes, & Di Beneditto, 2011). These dolphin-human

partnerships are reported from only two riverine/estuary systems, and the Brazilian example is documented to have arisen in 1847.

Isack and Reyer (1989) provide an in-depth study of communication between honeyguides and Boran pastoralists of Kenya, providing quantitative support for honey-hunters' claims that they can deduce the direction and distance to bee nests based on honeyguide flight patterns. The fact that Hadza follow honeyguides has been noted in a few publications (Crittenden, 2011; Marlowe, 2010; Wrangham, 2011), and a staged depiction of a Hadza "repaying" a honeyguide appears in a film (Benenson, 2014). Here, we provide the first quantitative, naturalistic study of Hadza honeyguide interactions.

While foraging, the Hadza try to attract honeyguides by shouting and whistling particular melodies (for a recording, see Wood, 2013b). Honeyguides emit a characteristic chatter or "guiding call" while leading Hadza, and they also use this call in ways that attracts people and compels them to begin following the bird. We observed two occasions (in camps #3 and #6, Table 1) in which a honeyguide flew directly into a Hadza camp and perched on a prominent tree, emitting its characteristic guiding call. This immediately caught the attention of those in camp who started whistling and talking to the bird ("Wait! Wait!"). Honeyguides more commonly attract honey-hunters outside of camp, by flying nearby, emitting their guiding call, whether men are whistling at the time or not. These observations generally correspond to reports from other study sites, where honey-hunters whistle and shout to attract honeyguides, and birds are also described as seeking out people to guide (Dean, Siegfried, & MacDonald, 1990; Isack & Reyer, 1989).

During a typical guiding sequence, a honey-hunter follows the bird as it swoops, widely fanning its feathers, from one perch to another, and the two engage in an ongoing exchange of whistles and chatter (for a recording, see Wood, 2013b). The honeyguide eventually perches near the nest of an *A. mellifera* colony, which is usually inside a tree. The honey-hunter then conducts a final search for the exact tree and nest location. After finding the nest, the honey-hunter lights a torch, climbs up to the nest entrance, blows in smoke to subdue the bees, chops open the tree with an axe, and reaches in for the honeycomb. While this happens, the honeyguide usually perches quietly nearby. The special nature of the Hadza-honeyguide relationship is attested to by the fact that honeyguides often perch comfortably within arrow-shot distance of Hadza, even though men hunt other bird species of similar size.

2. Materials and methods

The data reported here were collected during focal-individual observations carried out between 2006 and 2013 following 22 different Hadza men as they foraged for wild foods, on 40 separate trips, for a total of 212 hours. The average age of subjects was 32 years ($n = 40$, range = 17–54) on a per-observation basis, and 33 years on a per-subject basis ($n = 22$, range = 17–54). These focal-individual observations took place in 8 different Hadza camps (Table 1). The criteria for selecting a Hadza camp in which to collect data were two-fold: 1) that the Hadza living in the camp were foraging and subsisting on a diet of wild foods, rather than engaged in ethno-tourism or wage-labor, and 2) that the total set of camps was distributed across the regions that the Hadza occupy. Though our sample sizes are small for any given year or camp, we think they are broadly representative of Hadza habitats and foraging behavior because the observations are spread out among different years, seasons, regions, camps, individuals, and ages (Table 1).

During focal individual follows, a researcher observed a Hadza subject from the time he left camp to the time he returned to camp, continuously recording relevant behavioral data. Our methods involved the researcher quietly following and observing a single subject from an appropriate distance, providing no direction whatsoever to the subject as to where or how to forage or act. Where needed, and when doing so would not disturb the events taking place, the researcher asked the

Table 1
Camps, years, regions, seasons, and subjects of data collection. Numbered camps correspond to specific Hadza settlement locations. Regions are Hadza terms for prominent geographic areas, within which camps are found. Seasons are defined keeping with Marlowe and Berbesque (2009) as: early wet (Dec–Feb), late wet (Mar–May), early dry (Jun–Aug) and late dry (Sept–Nov).

Camp	Year	Region	Season	N adult male foragers in camp*	N focal follows	N focal follows with honey-guiding	N unique focal follow subjects	N unique focal follow subjects led by honeyguides
1	2006	Tli'ika	Early wet	9	2	2	2	2
2	2006	Tli'ika	Late wet	8	6	5	4	3
3	2006	Mangola	Late wet	11	4	1	4	1
3	2006	Mangola	Early dry	11	3	1	2	1
4	2006	Tli'ika	Late dry	7	12	3	3	2
5	2009	Han!abe	Late dry	6	4	0	2	0
6	2010	Tli'ika	Early dry	6	3	2	3	2
7	2010	Han!abe	Early dry	11	3	1	3	1
6	2011	Tli'ika	Early wet	15	1	1	1	1
6	2012	Tli'ika	Early wet	12	1	1	1	1
8	2013	Tli'ika	Early dry	4	1	1	1	1
Total				59**	40	18	22**	13**

* The totals in this column include all men aged 17 and above resident in the camps of observation who were foraging during our periods of observation; these totals do not include four elderly men who did not forage and thus could not be subjects of focal follows.

** Values in the 'total' row are sums of unique individuals in the total sample, while those of each camp-year-season row are sums of unique individuals during those period of observation.

subject questions to clarify observations. All of this was done in a quite and discrete manner to minimize observer effects. The data reported here only include behaviors involving interactions with honeyguide birds and the harvesting of bee nests. In general, we believe these behavioral domains are minimally influenced by the presence of the researcher: we did not increase or decrease the chance of a subject finding a nest, nor did we provide any direction to the subject before, during, or after the harvesting of bee nests.

During focal individual observations, the researcher recorded how many individuals were in a foraging party when the subject left camp, but thereafter, only recorded continuous observations of the focal individual. The presence of others was noted if there was a significant social interaction, such as when two individuals shared food with one another, or engaged in other acts of cooperation. The data recorded included times and locations of the following events: when subjects left camp; each instance in which a tree was inspected for the presence of a bee nest; whether tree inspections resulted in the subject finding a bee nest or not; encounters between honey-hunters and honeyguide birds; the start and finish of honeyguide follows; the species of bees in discovered nests; whether bee nests were harvested or not. When liquid honey was removed from a nest its volume was visually estimated, and it was noted whether such honey was placed into a storage vessel or was eaten. Any later eating of honey held in a storage vessel was similarly noted. These methods allow us to estimate the total caloric yield from each bee colony, and the fraction of all honey acquired that was eaten by subjects before retuning to camp. To help calibrate visual estimates of volumes, we used graduated cylinders to measure the volume of more than a hundred different food containers used in Hadza camps, and took pictures of these containers being held. This resulted in a reference set of scaled photographs of known volumes, which was carried by the researcher and referred to as needed during focal individual observations.

Volumes of honey were converted to weights assuming a density of 1.4 g/ml, (the average value reported in Ayodele, Folarin, and Oluwalana (2006)) and converted to caloric values following nutritional analyses of Hadza honey reported in Murray, Schoeninger, Bunn, Pickering, and Marlett (2001). When a comb containing honey or brood, or both, was removed from a nest it was recorded in terms of its length and width, and the percent of the comb filled with honey or brood.

In 2012, working in camp #6, measurements were made of honeycomb that men had brought back to camp, in order to develop Hadza-specific conversion factors between honeycomb sizes and caloric values. We first measured and weighed 10

randomly selected samples of brood-filled comb, and then weighed the wax that Hadza subjects expelled after eating the brood in these samples. From these data, we calculated that 1 square inch of comb contains 4.7 grams of brood on average, or 5.3 kcal following Finke (2005). Similarly, we measured and weighed 10 randomly selected samples of honey filled comb before the honey was eaten, and then weighed the wax that was expelled by Hadza after they had eaten the honey. These data indicate that 1 square inch of honey on comb contains 6.9 grams of honey on average, or 25.1 kcal following Murray et al. (2001).

3. Results

During 18 of the 40 focal individual observations, the subject followed a honeyguide at least once. Among all observations, subjects followed honeyguides 26 times, for a total of 329 minutes (3% of observed time), and found 18 *A. mellifera* nests with the bird's help, 16 of which they harvested (two were not harvested immediately because of aggressive bees and the hunter not carrying an axe, respectively).

There were 13 unique Hadza foragers in the set of 18 focal individual observations in which the subject followed a honeyguide at least once. Nine unique Hadza foragers harvested the 16 *A. mellifera* nests found with honeyguides. Among the 18 focal individual observations in which honeyguides were followed, 15 of these were of a honey-hunter who foraged solitarily throughout the entire period of observation. In two cases, the focal subject was traveling with a single other companion, and in one of those cases, they jointly followed the honeyguide bird. Finally, in one instance, the focal subject left camp with five other men, with the intention of cooperatively hunting zebra. This group only briefly followed a honeyguide bird, and then scared the bird away so that its guiding call would not alert the nearby herd of zebra to the hunters' presence.

Table 1 shows that 71% (10/14) of wet season focal individual observations included the subject following a honeyguide bird, while only 31% (8/26) of dry season observations did, indicating an unsurprising seasonal difference in honeyguide following (comparing dry vs. wet: $X^2 = 4.5$, $df = 1$, $p < .05$; comparing across four seasons: $X^2 = 10.3$, $df = 3$, $p < .05$). Just as honey production and acquisition typically increase in the wet season (Marlowe et al., 2014), so too do interactions with honeyguides.

By all measures, honeyguides greatly increased men's rates of finding and acquiring honey. When not led by honeyguides, Hadza encountered honey bee nests at a rate of 0.5 nests/hour, but while guided at a rate of 3.3 nests/hour, a 560% increase. Men inspected 554

trees for the presence of bee nests. When not guided, they experienced a 19% success rate of finding a nest upon tree inspection (101/523 tree inspections); while being guided, they had a significantly higher, 58% success rate, discovering 18 nests from 31 tree inspections ($X^2 = 24$; $df = 1$; $p < 0.001$).

Honeyguides' only led men to *A. mellifera* colonies, which produce the largest stores of honey of the 7 local bee species (others include small stingless bees in the genera *Trigona* and *Lestrimellitta*). This selectivity by the bird created a notable "honeyguide premium": men extracted on average 7,480 kcal ($se = 1,790$) from *A. mellifera* nests found with the help of honeyguides, compared to 1,390 kcal ($se = 277$) from all nests (*A. mellifera*, *Trigona* spp., and *Lestrimellitta* spp.) found without honeyguides (Wilcoxon rank sum $W = 1225$; $n_1 = 16$, $n_2 = 88$, $p < 0.001$). Focusing only upon *A. mellifera* nests, we find that honeyguides led Hadza to significantly higher-yielding nests than those they found without honeyguides, which yielded a lower 2,320 kcal on average (Figure, Wilcoxon rank sum $W = 206$; $n_1 = 16$, $n_2 = 17$, $p < .05$). The nest yield data underlying these analyses are provided in the supplementary material, available on the journal's website at www.ehbonline.org.

Because honey production, acquisition, and honeyguide bird encounters all increased in the wet season, it is worth investigating how nest yields varied by season. The 20 *A. mellifera* nests harvested in the wet season had an average caloric yield of 5,270 ($se = 1,100$) and the 13 harvested in the dry season had an average yield of 4,130 kcal ($se = 2,020$), a non-significant difference (Wilcoxon rank sum $W = 91$; $n_1 = 20$, $n_2 = 13$, $p = .15$). In a multiple linear regression analysis of *A. mellifera* nest yields with season (dry vs. wet) and honeyguide-assistance as independent variables, season had a non-significant effect upon nest yield (estimated effect of 'wet season' = -1,230, $p = .57$) while the assistance of honeyguides did have a significant effect (estimated effect of 'helped by honeyguide' = 5,660, $p < .05$, model adjusted $R^2 = 0.15$), supporting the hypotheses that honeyguides led men to higher-yielding nests of *A. mellifera* than those that men found on their own. More work would

be needed to learn whether the tendency of honeyguides to lead men to higher-yielding *A. mellifera* nests is due to such colonies simply being more bird-detectable (perhaps because of greater bee-traffic), or is due to selectivity by the birds.

In our observations, 49% (119,720/241,860 kcal) of all the honey and brood calories that men acquired came from nests found with honeyguides' help. Marlowe et al. (2014) estimate that 15% of the total food calories that Hadza consume *in camp* is honey. Because much honey is eaten outside of camp, the contribution of honey to the total Hadza diet is higher than the *in camp* figure. In our observations, men ate 27% of the total honey and brood they harvested out of camp (66,040/241,860 kcal). We therefore estimate that honey and brood comprises 16–20% of the total yearly diet of foraging Hadza, and that 8–10% of their total diet is acquired with the help of honeyguides.

Many depictions of the human-honeyguide relationship feature honey-hunters placing aside honeycomb for the bird's consumption after being led to a bee nest (e.g. Benenson, 2014; Chapin, 1924; Flannery, 2011; Grunton, 1990; Orians, 2014; Roosevelt, 1988; Spaarman, 1777; Stone, 2011; van der Post, 1962; Wrangham, 2011). Surprisingly, *not once* during this study did a Hadza ever place aside honeycomb for a honeyguide, or actively repay one in any way; on the contrary, if they ever acted to influence the bird's payoff, it was to reduce it. After Hadza men harvested honey from *A. mellifera* nests, they often fastidiously collected the honeycomb that remained lying about, and also hid, buried and burned honeycomb to prevent its consumption by the honeyguide (Table 2, and see Wood, 2013c for a video of such).

BW first observed a Hadza honey-hunter burying *A. mellifera* honeycomb in 2006, in camp #1. The follow subject was asked why he was doing this and he simply responded – "Tikiliko" (the Hadza name for *I. indicator*). Interestingly, in this particular case the honey-hunter had not been led to the bee nest by a honeyguide bird, and there was no honeyguide immediately present. However, this subject had followed a honeyguide bird earlier that day, and did so again later that day. Even when men find an *A. mellifera* nest on their own, and there is no honeyguide immediately present, they will carefully collect pieces of honeycomb that would otherwise remain discarded at the harvesting site. By doing so, the Hadza generally limit the meals that honeyguides foraging in the area might find and consume, which the Hadza believe increases the bird's hunger and motivation to guide.

During our observations, when men carefully collected pieces of honeycomb at honey harvesting sites, it was not always clear whether this represented active suppression of the bird's potential meal, or was done simply because the follow subject himself could later eat or share the honeycomb – both considerations were probably at work. In other cases, however, it was unambiguous that men were actively working solely to suppress the bird's food intake. In these cases, men collected honeycomb and then hid it in bushes, buried it, or burned it. We observed 7 such unambiguous cases, carried out by 5 individuals, in 4 camps, in which men clearly worked to limit honeyguide meals. Manipulating honeyguides in this way requires minimal work; it takes only a few seconds to collect, hide, bury, or burn honeycomb. These observations are tabulated in Table 2. It is worth noting that in 6 out of these 7 cases, the subject followed a honeyguide later on the same day, so the practice certainly did not preclude future honeyguide following.

Practicing the methodology of focal individual observations, we followed Hadza subjects when they walked from harvested bee nests, and thus we have no measures of the payoffs realized by honeyguides after men harvested the bee nests. Even so, we believe that the Hadza's expert ecological knowledge should be taken seriously, and that their calculated manipulation of honeyguides is likely to have the effect they believe it does. Each of the five subjects who was observed to hide, bury, or burn honeycomb explained to us, in discussions during the focal individual observation and in semi-structured interviews back at camp, that the reason they did so was to keep honeyguides' hungry, and thus more eager to guide them (for a video

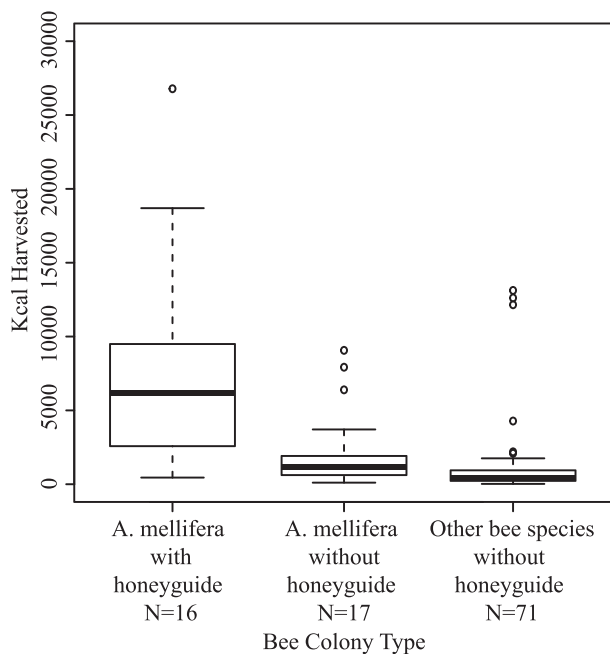


Figure. Kilocalories of honey and brood harvested from colonies of *A. mellifera* and other bee species, found with and without honeyguides' assistance. In this boxplot, rectangles enclose the data's inter-quartile range (IQR), midlines represent median values, and whiskers enclose the range of the data excluding outliers more than 1.5 IQR from the first or third quartile.

Table 2

Observations of men actively limiting honeyguide meals.

Camp	Action	Honeyguide immediately present?	Honeyguide followed earlier that day?	Honeyguide followed later that day?
1	Placed partially eaten honeycomb with brood deep inside tree cavity	No	Yes	Yes
2	Buried wax underneath branches and grass	Yes	Yes	No
2	Threw wax deep into bushes	Yes	Yes	Yes
2	Threw wax and brood deep into bushes	Yes	Yes	Yes
2	Buried honeycomb with brood under dirt and leaves	Yes	Yes	Yes
4	Gathered and placed expelled wax and dry honeycomb into fire, covered fire with grass tinder	Yes	Yes	Yes
6	Placed honeycomb with brood and expelled wax onto fire	Yes	Yes	Yes

of a man explaining his reasoning, see Wood, 2013a). Other Hadza who have been asked about this practice echo the same stated reasons.

3.1. Discussion: interspecific mutualisms

We have shown that the Hadza benefited from the bird's assistance; what did the honeyguides recoup from the relationship? Since our data were collected in a Hadza-centric manner, we unfortunately are not able to calculate the effect that Hadza had on the honeyguide's diet; but we can offer some relevant observations. Even though Hadza honey-hunters only acted to limit rather than increase the birds' payoff, they could not possibly have prevented honeyguides from eating all the scraps of honey or brood or wax that remained inside the now-exposed nests or scattered upon the ground. Honeyguides are small birds (~50 g, Friedmann, (1955)) and even a small intake of such scraps could compensate for the bird's guiding efforts. We agree with Sachs, Mueller, Wilcox, and Bull (2004) that an important reason why the human-honeyguide partnership is robust is because the bird is usually assured a benefit simply by the honey-hunter opening the nest entrance, allowing the bird to access honeycomb that would otherwise be inaccessible.

Comparative data indicate that interspecific mutualisms do not require active investments between the partners to evolve or be maintained (Connor, 1995). The cooperation between dolphins and fishermen that occurs in Myanmar and Brazil persists without any active "payments" by fishermen to their dolphin partners. Pryor and Lindbergh (1990:79) state that dolphins herd fish towards fishermen casting nets and then "take advantage of the confusion which the falling nets cause among the fish schools to catch fish for themselves" and that following a catch, fishermen "never give them fish". The benefits to the dolphins appear to be incidental by-products of the self-serving behavior of the fishermen, a form of "by-product mutualism". Even if they do not provide active food repayments, the fishermen in Myanmar, like the Hadza, provide a less overt form of investment into the well being of their animal partners, in the form of strategically restrained predation (Tun, 2004:47).

Of course, people extensively manipulate the diets of domesticated animals, and suppressing the diet of a hunting or guiding animal might be an especially useful tactic. In a manner somewhat analogous to the Hadza's treatment of honeyguides, in a variety of cultures, hunting dogs are sometimes "kept hungry" prior to a hunt (Herzog & Vasyukov, 2010; Menache, 1998).

3.2. Discussion: the evolution of human-honeyguide interactions

Dean et al. (1990) show that even though a supposed partnership between honey-badgers and honeyguides has often been repeated in print, actual credible observations of such are non-existent. A possibility not considered by Dean et al. (1990) is the idea proposed by Friedmann (1954) – that baboons might partner with honeyguides. Again, no credible observations of this partnership have been

published. We contacted six principal investigators at sites of long-term baboon research and asked whether they had ever observed baboons interacting with honeyguides, and all six reported never witnessing such (J. Altman, S. Alberts, R. Palombit, R. Cheney, D. Seyfarth, and L. Swedell, personal communication, 2013). In summary, there exist no credible first-hand reports of any species other than humans having been led to a bee nest by a honeyguide.

Since humans are the only species attested to partner with honeyguides, this would suggest that humans, or our ancestors, were the partners of proto-honeyguides as the habit evolved. This idea was first proposed by Hoesch (1937), was seconded by Dean et al. (1990) and recently endorsed by Wrangham (2011). The ecological and technological factors that contributed to the evolution of this relationship are unknown, but the behavioral ecology of non-human primates, hunter-gatherers, and bees does offer some clues, which we use as the basis for an evolutionary model.

Even without any way to directly assess human-honeyguide interactions in the past, we believe it is still credible to propose that the relationship has, over time, evolved from one that is simple and common in nature – commensalism – to one that is more complex and rarer: manipulative mutualism (Connor, 1995). We propose that in a first, commensal phase, honeyguides preyed upon the bee nests and discarded honeycomb that hominins made available through their honey hunting. In a second, mutualistic phase, honeyguides evolved the habit of actively leading hominins to bee nests. Finally, in a third phase of manipulative mutualism, hominins began to actively change the payoffs received by honeyguides – either by actively "rewarding" them or by reducing their immediate payoff. The Hadza we observed did not actively reward honeyguides, but such may occur in other contexts. Below, we provide suggestions for how these interactions initially arose, and how transitions between the three stages took place, based on theory and available evidence.

Based on within-species mtDNA variation, Spottiswoode, Stryjewski, Quader, Colebrook-Robjent, and Sorenson (2011) conservatively estimate that *I. indicator* is at least 3 million years old (see also Wrangham, 2011 on this topic). We think it is reasonable to assume that an initial commensal association between hominins (*Ardipithecus ramidus* or an Australopithecine) and honeyguides arose in the Pliocene.

Humans, chimpanzees, orangutans, and capuchins have all been observed in the wild using sticks to probe and extract honey from the nests of small stingless bees (Meliponinae) (Brewer & McGrew, 1990; Moura & Lee, 2004; Sanz & Morgan, 2009; van Schaik, Fox, & Sitompul, 1996). Chimpanzees prey upon *A. mellifera* colonies more frequently than any other non-human primate (Wrangham, 2011), and they use distinct tools to probe, open, extract honey and brood from nests, swat away, and kill bees (Boesch & Boesch, 1990; Sanz & Morgan, 2009; Wrangham, 2011). An early hominin such as *Ardipithecus ramidus*, which possessed both arboreal and bipedal adaptations at 4.4 MYA (White et al., 2009), probably also actively foraged for the honey of stingless bees and occasionally that of *A. mellifera*, aided by simple tools.

Environmental changes during the last three million years may have led to an increase in the availability of *A. mellifera* honey in the range of hominins, and corresponding increases in honey consumption and commensal interactions with honeyguides. During the Pliocene, a climatic shift towards drier and cooler conditions led to the expansion of more open, savanna habitats across many parts of Africa (deMenocal, 1995). These large-scale changes in plant communities would have altered the biogeography of insect pollinators, including bee species. Standing trees are the preferred nest locations for nearly every species of honey-producing bee in Africa (Hepburn & Radloff, 1998). More open habitats, with more widely spaced nest locations, would give pollinators with wider foraging ranges a relative advantage over those with smaller ranges. Foraging range is known to scale positively with body size among bee species (Greenleaf, Williams, Winfree, & Kremen, 2007; Zurbuchen et al., 2010), and *A. mellifera* is larger than all other honey producing bees in Africa (Michener, 2000). Single colonies of *A. mellifera* in Botswana have been recorded to forage over areas 55–80 km² (Schneider, 1989) and honey bees have been reported to have a maximum foraging radius of 13.5 km (von Frisch, 1967). Its wide foraging range, generalist foraging habits, and complex social behavior would have given *A. mellifera* an advantage in open habitats over its competitors, including the smaller stingless bees. While *A. mellifera* and stingless bees are found in both forests and more open savanna habitats, stingless bee diversity is greatest in moist tropical forests (Michener, 1979). Across Africa today, the principal plant genera that *A. mellifera* forages upon are more abundant in savanna environments than in forests (Hepburn & Radloff, 1995).

Most chimpanzee communities live in forests, but those of Mt. Assirik, Senegal, occupy an open habitat, with over half of the study area covered with grassland, and only 3% by forest (McGrew, Baldwin, & Tutin, 1981). Interestingly, these savanna-dwelling chimps appear to eat more *A. mellifera* products than forest-living chimps. *A. mellifera* remains were found in 23% of Assirik chimp feces (McGrew, 1983), while fecal analyses of forest chimpanzees in both the Democratic Republic of Congo and Uganda revealed bees or bee products in only 3% of their feces (Stanford, 2006; Wrangham, 2011; Yamagiwa & Basabose, 2006).

Today, Greater Honeyguides avoid lowland forest habitats, and occupy only savannah, shrubland, forest edges, and open woodlands (Short & Horne, 2001). The earliest interactions of hominins and proto-honeyguides probably occurred in such habitats. It is likely that proto-honeyguides would not have led, but instead followed and scrounged from early hominins, as they inadvertently dropped honeycomb to the ground or left it behind in partially harvested nests. When Chimpanzees attempt to harvest honey from *A. mellifera* nests, they commonly abandon the nest before exhausting its stores of honey and brood due to attacking bees (Goodall, 1986). If early hominins foraged for *A. mellifera* in a similar manner, then they would have provided rich opportunities for scrounging proto-honeyguides.

The hypothesis that drier, more open habitats led to a competitive advantage for *A. mellifera* and an increased availability of honey in the range of hominins deserves further scrutiny. If true, then hominins occupying these habitats would have likewise increased their consumption of highly nutritious and easily digestible *A. mellifera* honey, resulting in increased interactions with proto-honeyguides.

For at least 2.6 million years, hominins have manufactured stone tools (Plummer, 2004), which surely enhanced their ability to access *A. mellifera* nests. The control of fire and smoke, which is at least 1 million years old (Berna et al., 2012), would have further increased hominin's honey-hunting capacity, giving them a means to calm the bees while destructively opening up their nests (Wrangham, 2011). As hominins became more technologically adept at opening and exhausting the nests of *A. mellifera*, the payoff to proto-honeyguides that simply scrounged from hominins would have declined. In this context, the guiding habit is likely have been positively selected, because as per-nest payoffs to the bird declined, so too did the

marginal benefits of accessing second or subsequent nests. Active guiding would permit the bird to have realized these gains, and would also have provided a mutualistic benefit to the honey-hunter.

A third phase, of manipulative mutualism, arose when humans began actively changing the payoffs that honeyguides received – by investing either in the bird's increased or decreased food intake after nests were harvested. Either of these strategies might be useful in different contexts. Ecologically, we would expect that people who regularly harvest honey from the same area, and who experience greater food scarcity, should be more likely to limit the bird's payoff, in order to maximize their own long term diet drawn from the local area. Individuals who less frequently harvest honey from a locale, or who have greater food security, should be more likely to leave rewards for honeyguides, perhaps as a way to develop a bird's latent guiding habit or to re-enforce one infrequently expressed.

Effective foraging for high quality but difficult-to-acquire foods has been proposed as one of the selective forces underlying the expansion of human brain size over the last two million years (Kaplan, Hill, Lancaster, & Hurtado, 2000). On this note, Hadza honey-hunters' interactions with honeyguides clearly illustrate an appreciation of the bird's motives, and a cunning application of social intelligence.

4. Conclusion

Our data show that when Hadza followed Greater Honeyguides, their honey-finding efficiency greatly increased, and the bird lead Hadza to higher-yielding nests of *A. mellifera* than they found without the help of honeyguides. We estimate that 8–10% of the Hadza's total diet is acquired with the help of honeyguides, illustrating the importance of this relationship.

First-hand reports only attest to humans being led by honeyguides, and so humans or our hominin ancestors appear to be the most likely partners of proto-honeyguides, as the habit evolved. Our interpretation of available evidence leads us to suggest that the earliest associations of hominins and honeyguides probably occurred during the Pliocene, and then steadily increased in frequency as savanna habitats expanded, hominins began fashioning stone tools, and gained control over fire. Honeyguides are proposed to have initially associated with hominins as commensals, and to later have evolved the active guiding habit as *Apis mellifera* honey became a larger part of the hominin diet. The manipulation of honeyguides that we witnessed probably arose relatively late, after the guiding relationship had evolved between the bird and a less cognitively sophisticated hominin. The fact that the Hadza do not actively repay honeyguides but instead suppress their diets illustrates that cooperation can endure between people and other species under a robust range of conditions.

Supplementary Materials

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2014.07.007>.

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