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# 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.



## 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 consumption[1]. Honey forms an important part of the diet of many

[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.

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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; Orians, 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 truncates* 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