CULTURAL COEVOLUTION

Culturally determined interspecies communication between humans and honeyguides

Claire N. Spottiswoode[1,2]*† and Brian M. Wood[3,4]*†

Species interactions that vary across environments can create geographical mosaics of genetic coevolution. However, traits mediating species interactions are sometimes culturally inherited. Here we show that traditions of interspecies communication between people and wild birds vary in a culturally determined geographical mosaic. Honey hunters in different parts of Africa use different calls to communicate with greater honeyguides (*Indicator indicator*) that lead them to bees' nests. We show experimentally that honeyguides in Tanzania and Mozambique discriminate among honey hunters' calls, responding more readily to local than to foreign calls. This was not explained by variation in sound transmission and instead suggests that honeyguides learn local human signals. We discuss the forces stabilizing and diversifying interspecies communication traditions, and the potential for cultural coevolution between species.

Species interactions such as mutualism, parasitism, and predation have generated much of life's diversity, playing out differently on different ecological stages in a geographical mosaic of genetic coevolution (*1*). However, interspecies interactions are often mediated by phenotypically plastic traits, including learned traits that vary geographically (*2*). Traits shaped by social learning can form stable cultural traditions in diverse animal species from humans to fruit flies to sperm whales, and these can vary markedly among populations (*3*). An intriguing, yet understudied, scenario may arise where two (or more) species reciprocally influence one another's fitness in an interaction mediated by learned traits in both species. Learned responses in one species could thus reinforce the learned traditions of the other, culminating in a process of interspecies cultural coevolution (*4*–*6*).

Humans have an unrivaled capacity for social learning (*7*). Our species' cultural adaptability has allowed us to invade new environments and dominate landscapes (*8*), and produces diverse behavioral responses in wild nonhuman species (*4*, *9*). In Africa, we should expect the longest periods of interaction between humans (or our ancestors) and other species. Here we investigated how human cultural traditions mediate an ancient, cooperative interaction between humans and a wild bird. Specifically, we asked whether geographically varying, learned traits facilitated mutualistic cooperation, and thus set the stage for cultural coevolution to occur.

We investigated interspecies communication between humans and greater honeyguides (*Indicator indicator*) (hereafter "honeyguides"), which lead people in Africa to wild bees' nests (*10*, *11*). Honeyguides naturally locate bees' nests and eat wax. Humans can subdue the bees and open their nests, thus exposing beeswax for the honeyguides and honey for themselves. Honeyguides across Africa give distinctive chattering calls to attract people and then indicate the direction to bees' nests by flying from tree to tree (*5*, *11*). Honeyguides thus exchange their knowledge of bees' nest locations for honey hunters' exceptional skills at subduing bees (typically using smoke), opening nests and exposing edible wax and bee brood. Humans possess technological, cognitive, and social capabilities that make us highly efficient honeyguide partners (*11*). Our hominin ancestors, like great apes today, would likely have eagerly sought honey (*12*, *13*). Their ability to acquire it would have been enhanced by stone tools (in use since 3.3 million years ago) and the mastery of fire (between 1.5 million and 350,000 years ago) (*13*–*16*). Recent changes now threaten the viability of the partnership, including apiculture, urbanization, increased availability of refined sugar, and exclusion of people from protected areas (*17*–*19*).

Where this partnership persists, marked cultural variability exists in the traits that mediate it, including how people attract honeyguides. Honey hunters often use specialized calls to advertise that they are looking for a honeyguide partner and to maintain cooperation while following a guiding bird. In one population, honeyguides have been shown to be more likely to cooperate with humans giving this signal (*5*). Honey hunters from the Yao cultural group in northern Mozambique typically give a loud trill followed by a grunt ("brrrr-hm") when seeking and following honeyguides (*5*), whereas honey hunters f
the Hadza (also known as Hadzabe) cult
group in northern Tanzania use a melodic whistle (*16*) (examples in audio S1), and other cultures elsewhere in Africa use different, distinct calls in the same context (*11*, *20*–*22*). Members of the honey-hunting communities that inspired this study report that they learn these calls from their fathers or other elders, and that no-one diverges from these traditions because they will find less honey if they do (*5*).

Here we ask whether honeyguides are attracted to local rather than foreign honey-hunter signals, which would suggest that they learn the cultural traditions of mutualistic interactions with humans. Honeyguides' propensity to guide humans appears to be innate, as they attempt to guide within weeks of fledging parasitically from other species' nests, and to guide humans in regions where people rarely follow (*23*, *24*). However, it can either diminish or be reinforced on the basis of variable interactions with people (*23*). A priori, we expect that preferences for specific human signals would be learned by honeyguides, rather than arise though genetic local adaptation (*5*). In other contexts, songbirds learn and recognize local vocal dialects used by social group members (*25*, *26*). Greater honeyguide populations across Africa do not exhibit any obvious phenotypic or nuclear genetic divergence (*27*, *28*), consistent with high rates of gene flow. Alternatively, all honeyguides may be innately attracted to a range of honey-hunter signals, regardless of their prior exposure to them. We developed simple game-theoretic and optimal foraging models to explore why these interspecies communication traditions are consistent locally but vary between cultures.

Honeyguides have learned the signals of their local human partners

We conducted field experiments to ask whether honeyguides are more likely to initiate cooperation [i.e., approach a human and give distinctive guiding calls and behavior (*11*)] in response to signals of their local human culture, than to those of a foreign culture, or to arbitrary human sounds that serve merely as a cue of human presence. Following previously established methods (*5*, *29*), we carried out experimental transects simulating honey-hunting forays in Niassa Special Reserve in Mozambique ($N = 77$ transects of 15 min each) and in the Kidero Hills of northern Tanzania ($N = 75$ transects of 30 min each; longer transects were designed because we anticipated, and found, a lower density of bees and honeyguides in this drier environment). On each transect we played back one of three types of sounds (examples in audio S2): the Yao honey-hunting signal, the Hadza honey-hunting signal, or an arbitrary human sound (a honey hunter calling his name,

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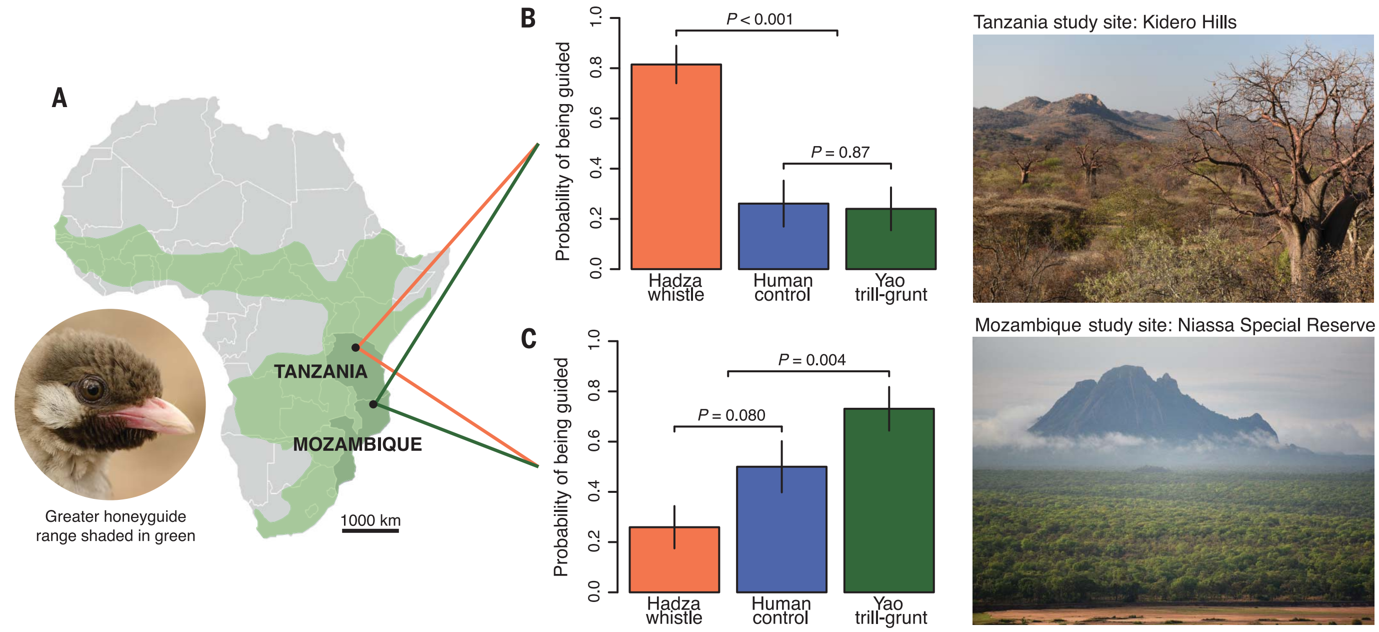

Fig. 1. Honeyguide cooperative behavior in response to experimental acoustic playbacks. We carried out the same experimental treatments at (**A**) Kidero Hills inhabited by Hadza people in Tanzania and Niassa Special Reserve inhabited by Yao people in Mozambique. Values are probabilities of honeyguides initiating cooperation with humans on (**B**) a 30-min search (Tanzania) or (**C**) a 15-min search (Mozambique), giving either Hadza (orange) or Yao (green) honey-hunting signals, or arbitrary human sounds (blue). *P*-values result from planned comparisons of response rates. Error bars span ±1 SE.

alternating across transects between Yao and Hadza voices, which were acoustically similar; fig. S1). We performed the same treatments, using the same set of playback exemplars, at both sites (Fig. 1A).

We found that in Tanzania, there was a 3.26 times higher probability of honeyguides initiating cooperation in response to local Hadza whistles (81.5% of transects) than to either foreign Yao trill-grunts (24%) or control sounds (26.1%) [Fig. 1B; logistic regression planned comparison (*30*) of local signal with foreign and control sounds, slope ± SE = 1.72 ± 0.40, $Z = 4.32$, $P < 0.0001$]. Honeyguides in Tanzania responded similarly to foreign Yao trill-grunts and to control sounds (slope ± SE = −0.06 ± 0.33, $Z = -0.17$, $P = 0.87$). In Mozambique, there was a 1.96 times higher probability of honeyguides initiating cooperation in response to local Yao trill-grunts (73.1% of transects) than to foreign Hadza whistles (25.9%) or control sounds (50% of transects) (Fig. 1C; logistic regression planned comparison of local signal to foreign and control sounds, slope ± SE = 1.02 ± 0.36, $Z = 2.85$, $P = 0.004$).

At each site, we also evaluated models with time of day and temperature variables, but they did not improve predictive accuracy (*29*). Acoustic treatment alone explained 36% and 20% of the variation in honeyguide response in Tanzania and Mozambique, respectively.

These results enable us to compare three hypotheses: that honeyguides have learned the culturally varying signals of their local human partners (learning); that honeyguides have innate preferences toward these sounds (sensory bias); or that certain sounds transmit better in different environments [sensory drive (*31*, *32*)]. Results are consistent with learning and sensory drive, but not sensory bias, because if Yao and Hadza honey-hunting signals were intrinsically attractive to honeyguides, honeyguides should respond most to both signal types at both sites.

To separate learning from sensory drive, we measured the acoustic attenuation of each playback exemplar in each environment, to test two predictions from the latter hypothesis: (i) Signals should attenuate faster in the foreign than local environment, and (ii) attenuation rates of exemplars should predict honeyguide responses. Results indicated that Hadza whistles attenuated the least, but all sounds attenuated similarly across environments (Fig. 2 and table S1). Therefore, honeyguides were not more likely to hear local signals given in their local habitat. Second, models that include the attenuation rates of exemplars (in the relevant environment) explained no additional variation in results (table S2). Thus, sensory drive is not a viable explanation. Our results are most consistent with the learning hypothesis, that honeyguides learn to prefer the signals used by their own local human partners.

Stability and diversity in interspecies signals

Why do stable traditions of interspecific communication arise, and why might they vary across cultures? Honeyguides respond adaptively to culturally varying human signals (Fig. 1), highlighting the benefits of mutual intelligibility. This should provide an incentive for signal stability across time. As honey hunters attest, once a local tradition of honeyguide–human communication is established, it would not pay a honey hunter to radically diverge from that tradition. Our data suggest that a honey hunter who changed their whistled signal to a trill-grunt in the Hadza region would find less than half as much honey (Fig. 3).

We used a game-theoretic model [(*29*), model 1] to confirm that these benefits of mutual intelligibility create a coordination game (*33*) in which the evolutionarily stable strategy is for the honey hunter to produce, and the honeyguide to respond to, the same local signals.

Next, we consider why signal forms might differ across cultures. The sounds that people use to signal to honeyguides vary greatly among cultures (*5*, *11*, *16*, *21*, *22*), including within 100 km of our study sites (*20*). We suggest that these differences may not always be arbitrary, because the ways that people interact with honeyguides are influenced by differing cultural histories and economic practices. The Hadza speak Hadzane, a language isolate reflecting their distinctive cultural heritage and genetic descent from hunter-gatherers who lived in the region before the arrival of herders and farmers over the last 4000 years (*34*–*36*). The main economic pursuits of Hadza men are collecting wild honey and hunting animals (*36*, *37*). While honey hunting, Hadza

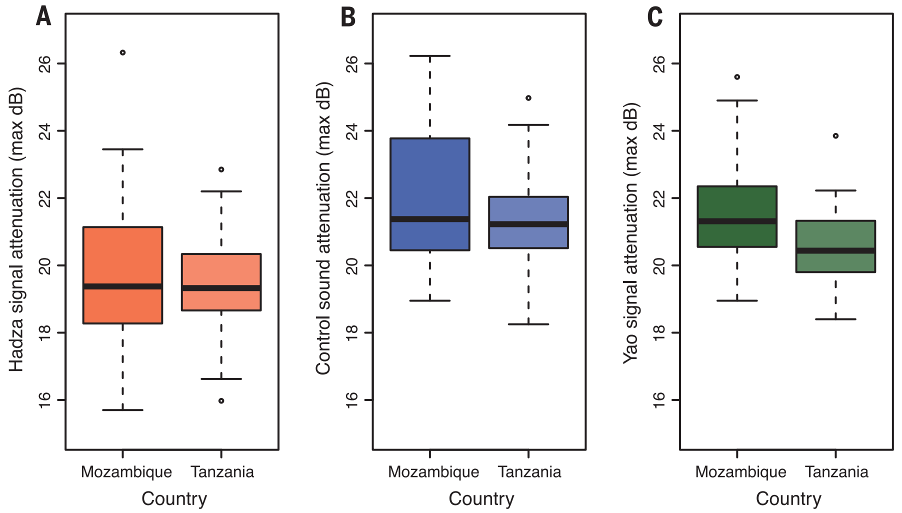

Fig. 2. Acoustic attenuation of honey-hunting signals used by different human cultures, and controls. (**A**) Whistles used by Hadza people in Tanzania, (**B**) arbitrary human sounds, and (**C**) trill-grunts used by Yao people in Mozambique all attenuate similarly from 3- to 30-m distance in their local environment compared to the foreign environment (maximum amplitudes of 77 sounds from different individuals played back in each environment; treatment × country interaction in linear model *P* = 0.90; table S1). Results were similar for mean amplitudes (table S1).

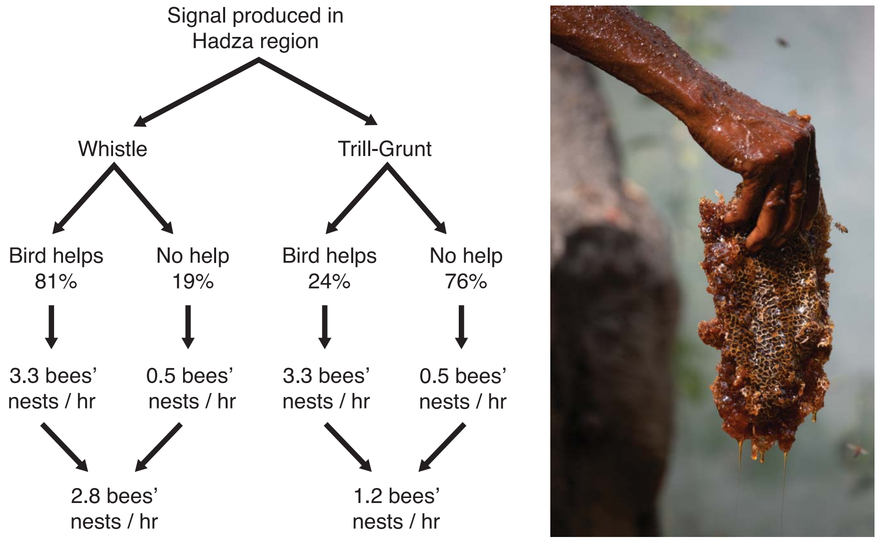

Fig. 3. The expected payoffs to whistling or trill-grunting in the Hadza region. Probabilities of guiding are taken from this study (Fig. 1). In a prior study, Hadza honey hunters found bees' nests at a rate of 3.3 per hour when helped by honeyguides, and 0.5 per hour without their help (*16*). A honey hunter in the Hadza region who committed to whistling to attract honeyguides for 30 min would be expected to find bees' nests at a rate of 2.8 per hour (0.81 × 3.3 + 0.19 × 0.5), whereas one who trill-grunted would realize a rate of 1.2 per hour (0.24 × 3.3 + 0.76 × 0.5). Bees' nests found with honeyguide assistance also yielded more honey than those found without honeyguides (*16*).

men also carry bows and arrows, and if prey are encountered, they quietly stalk them (*38*). Hadza hunters thus confront a trade-off between attracting honeyguides and not being detected by prey that fear human voices (*39*). In interviews carried out between 2015 and 2021, men stated that one reason they use whistles is to "sound like birds" (movies S1 and S2). Similarly, Hadza hunters also occasionally use whistles to communicate with other hunters. If whistles disguise human presence from game animals, Hadza hunters might plausibly be predisposed to whistling to attract honeyguides, rather than using vocal signals like those of the Yao, which are recognizably human, as confirmed by acoustic analysis (figs. S2 and S3). A nonmutually exclusive alternative is that whistles attenuate less (Fig. 2) and so better elicit cooperation where honeyguide densities are lower. These hypotheses parallel accounts of cultures worldwide that use whistled speech to (i) evade detection by game animals and prevent eavesdropping by outsiders, and (ii) communicate over long distances (*40*, *41*).

By contrast, the Yao speak an eastern Bantu language related to that of other agriculturalists in eastern Africa (*42*). In Niassa Special Reserve, farming and fishing are the main economic pursuits, supplemented by honey hunting, which a subset of adult men regularly undertake to generate cash and supplement household diets. Yao honey hunters here do not hunt mammals and are more concerned with avoiding dangerous animals (elephants, buffalo, lions). The conspicuousness of the signal they use could plausibly benefit them by scaring off these widely feared animals. Future research should test whether Yao trill-grunts broadcast human presence to mammals, and Hadza whistles disguise it. We did not design the current study to test these ideas, but note that at Niassa, there is a nonsignificant trend in which honeyguides responded to Hadza whistles less often than to control sounds of human presence (Fig. 1C). We investigated the competing demands of signaling to honeyguides and concealing cues from prey in an optimal foraging model [(*29*), model 2]. This suggests that the importance of mammal hunting could influence signal form in human–honeyguide communication.

Cultural coevolution of communication

Our field experiments and modeling suggest that honeyguides and humans influence one another through learned traits that culturally vary across different human populations (Fig. 1), while consistency within populations is maintained by the benefits of coordination (Fig. 3 and table S4). This leads to a learned communication system that makes honeyguides more likely to interact with a cooperative human, and humans more likely to elicit cooperative behavior from a honeyguide. Learned conventions thus maintain mutualistic coordination and discourage local people or birds from deviating from them. Thus, just as social conventions arising from coordination games lead to stability in word choice (*43*) and facilitate cooperation in humans (*33*), they likely also facilitate mutualistic interspecies cooperation.

These results are consistent with several predictions of a hypothesis of "cultural coevolution" between species (*4*). We find that cultural traditions in one species favor consistent learned responses in another species, which in turn reinforces the cultural traditions of the first.

There is evidence of cultural transmission of these traits through social learning in at least one species (humans) (*5*, *23*). Another criterion for cultural coevolution is that honeyguides also socially learn, a plausible hypothesis that is yet to be tested (*5*). In other bird species (*26*), preferences for conspecific local dialects are socially learned. Honeyguides have abundant opportunities for social learning because many honeyguides, including juveniles, are attracted to the sounds, sights, and smells of guiding events and honey harvests, and aggregate to scrounge from wax left behind (*44*, *45*). Social learning would benefit honeyguides as it is more efficient than individual learning in allowing a relatively large honeyguide population to learn the signals of a relatively small honey-hunter population. Honeyguide social learning could thus accelerate phenotypic adaptation to human cultural shifts in space or time (*4*), in turn favoring humans who shift to the new tradition. Such reciprocal reinforcement might operate in other examples of culturally-dependent interactions between humans and wildlife, both cooperative (*23*, *46*) and antagonistic (*47*), and between interacting nonhuman species. Cultural coevolution may form geographical mosaics that generate and maintain cultural biodiversity, just as geographical mosaics of genetic coevolution generate and maintain genetic biodiversity (*1*).

Culturally determined interspecies communication has implications for the evolution of cooperation. Once learned by honeyguides, culturally varying human signals facilitate honeyguides' ability to choose a good honey-hunter partner and thus increase the payoff from the mutualism for both species. This accords with our understanding that phenotypic plasticity can stabilize mutualisms, by facilitating choice of cooperative partners (*2*). Cultural traditions of consistent behavior are widespread in nonhuman animals (*3*) and could plausibly mediate other forms of interspecies cooperation. Reciprocal phenotypic plasticity through learning could thus facilitate mutualisms across generations and set the stage for stronger selection on adaptations linked to mutualisms (*2*).

Our experimental data show that a mosaic of interspecies communication traditions exist between people and birds, underpinned by learning in both species. The human–honeyguide partnership thus represents an ancient form of culturally dependent biodiversity (*19*, *23*). Any effort to help sustain these threatened interspecies partnerships should be based on an understanding of the forces shaping local traditions and generating geographical diversity (*19*, *48*).

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SUPPLEMENTARY MATERIALS

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MDAR Reproducibility Checklist
Audio S1 and S2
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Editor's summary

Honeyguides, a species of African bird, are well known to guide other species to beehives. They have even been known to work with honey badgers, but their closest and most successful collaborators are humans. Several indigenous African groups work with these birds across their range. Looking at these interactions in Tanzania and Mozambique, Spottiswoode and Wood have shown that honeyguides respond more readily to the specific calls of their local honey-hunting partners than they do to the calls of honey hunters from other regions (see the Perspective by Searcy and Nowicki). Thus, honeyguides appear to learn the calls of their local partners, and honey hunters maintain these successful calls over generations. —Sacha Vignieri

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Supplementary Materials for

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The PDF file includes:

Materials and Methods
Supplementary Text
Figs. S1 to S3
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Other Supplementary Material for this manuscript includes the following:

MDAR Reproducibility Checklist
Audio S1 and S2
Movies S1 and S2

Materials and Methods

Study sites

Greater honeyguides inhabit savannah woodland habitats in much of sub-Saharan Africa. Our two study sites were in eastern Africa. First, the Kidero Hills, Arusha Region, Tanzania, a region where the Hadza people live. The habitat here is semi-arid thornbush thicket with numerous baobab trees *Adansonia digitata*. The Kidero Hills are also home to the Datoga people, who unlike the Hadza, are pastoralists and do not honey-hunt, but instead commonly trade with Hadza to acquire honey. We conducted field experiments within an approximately 100 km^2 area in the Kidero Hills, located between Lake Eyasi and the Yaeda Valley and centred on approximately 3°52'S, 35°01'E, during 14–24 July 2017. We have conducted research here since 2004, and collected sound recordings for experimental playbacks in 2016. Second, Concession L5 South of the Niassa Special Reserve, Niassa Province, Mozambique, inhabited by the Yao people (other parts of the Niassa Special Reserve are inhabited by Makua as well as predominantly Yao people). The habitat here is primarily deciduous miombo woodland punctuated by granite inselbergs, with mixed savannah woodland including baobab trees along drainage lines (*44*). We conducted field experiments within an approximately 160 km^2 area between the Lugenda, Mbamba and Msanjesi rivers, centred on approximately 12°07'S, 38°07'E, during 29 November to 18 December 2016. We have conducted research here since 2013, and collected sound recordings for experimental playbacks in 2015 and 2016. Greater honeyguide density in a subset of this study area was 16.6 individuals/km^2 (*45*). At both sites, honey-hunting is conducted year-round, with peaks at the beginning and the end of the dry season (May–November).

Field experiments

Experiments at both sites followed exactly the same protocol (following ref (*5*)), except that experimental trials ceased after 15 minutes in Mozambique and after 30 minutes in Tanzania, which is a drier environment where we anticipated a lower density of bees and honeyguides, and so preliminary studies indicated longer trials were needed to detect differences in honeyguide preference. Experimental transects commenced between 07:55–11:42 (i.e. 1.1–4.9 h after sunrise) and 16:05–17:38 (1.1–2.6 h before sunset) in Tanzania, and between 05:33–09:46 (i.e. 0.7–4.9 h after sunrise) and 14:53–16:25 (1.3–2.9 h before sunset) in Mozambique. Starting locations of each experimental transect were selected a priori using Google Earth, and began along a vehicle track to minimise prior cues of walking humans prior to the transect start. Each transect started a minimum of 500 m from previous transects, and a minimum of 1500 m for transects conducted on the same day to minimise the chance of interacting with the same bird twice (see (*5*) for data on biological justification). During each transect, an observer (BMW or CNS in Tanzania and CNS in Mozambique) and two local honey-hunters, one ahead of and one behind the observer, walked in an approximately straight line (with occasional detours to avoid elephants or impenetrable thicket) at normal foraging pace, in silence except for the observer playing back experimental sounds using a speaker (see Experimental acoustic treatments). Trials began after an initial 30 second walk in silence from the vehicle, to allow any honeyguide attracted by the vehicle noise (i.e. independently of our experimental playback) to initiate guiding before the experiment began; if this happened, the trial was abandoned. In Mozambique, trials ceased at the end of a 15 min linear transect; in Tanzania, we turned back at 15 min, continuing playback, and approximately retraced our steps until 30 min had elapsed. Trials ceased at 15 min or 30 min respectively if no honeyguide guided us, or when a honeyguide initiated guiding behaviour. The guiding bird was without exception first detected by the honey-hunters. In the Mozambican trials, all 38 guiding birds were in fully adult plumage; of the birds we could sex visually based on plumage, 10 were female and 26 were male. In the Tanzanian trials, 7 of 34 guiding birds were in detectibly immature plumage. suggesting they were first-year birds (this accords with the timing of the experiments relative to the honeyguide breeding season); of the birds we could sex visually based on plumage, 10 were male and 20 were female. When a honeyguide initiated guiding, we marked the location using GPS, and followed the bird while continuing playback at slightly lower amplitude to mimic natural human behaviour, until we found a bees' nest or abandoned the search because the honeyguide ceased guiding us (as judged by the honey-hunters). At the end of each trial, we measured air temperature using two Lascar EL-USB-1-LCD temperature loggers (RS Components, Corby, UK) (in Tanzania) or three standard air thermometers (in Mozambique) suspended in the shade of a tree, about 1.5 m above the ground. Mean ±SE air temperatures were 27.6 ±0.40 °C (range 18.5–33.3) in Tanzania, and 30.6 ±0.41 °C (range 23.4–39.0) in Mozambique.

Permits

Research in Tanzania was conducted with permission from the Tanzania Commission for Science and Technology (COSTECH) (permit numbers 2016-174-NA-2000-80 and 2016-287-NA-2000-80). We also received local approvals from the Hadza communities of Domanga, and the villages of Domanga and Endesh. Research in Mozambique was conducted with permission from the Administração Nacional das Áreas de Conservação (permit number 11/11/2016).

Experimental acoustic treatments

Sounds were played back on a continuous loop using an SME-AFS speaker (Saul Mineroff Electronics, Elmont, New York) and a Sony M10 digital recorder at consistent amplitude. Exemplars were recorded at 3 m using a Sennheiser ME66 shotgun microphone and a Sony M10 digital recorder, as 48 or 44.1 KHz, 32-bit WAV files. We first cleaned field recordings by applying a low cut filter at 100 Hz in the RavenPro software 1.5 (*49*) to remove low-frequency noise, and normalised peak amplitude to -7 dB using the software Audacity. To ensure that playback amplitude was consistent when emitted from the speaker, we standardised output by manually adjusting the speaker volume setting until peak amplitude measured as 83.7 dB at 3 m (the mean amplitude of Yao signals at 3 m). We measured amplitudes using an NTi XL2 sound level meter and acoustic analyser with associated M4260 microphone (NTi Audio, Schaan, Liechtenstein), placed on a tripod 1.35 m above the ground. Each transect used a unique recording of a different Yao or Hadza honey-hunter. Acoustic treatment type was randomly allocated immediately before the start of each transect. Treatments were as follows: (i) Hadza honeyguide signal, i.e. a melodic whistle, recorded in our Tanzanian study area in 2016 and 2017; (ii) Yao honeyguide signal, i.e. "brrrr-hm", recorded in our Mozambican study area in 2015 and 2016; or (iii) control human sound, i.e. a Hadza or a Yao honey-hunter (at both sites, alternating playbacks between cultural groups) shouting his name, recorded from the same individual people as the two signal types above. Some of the playback exemplars for treatments (ii) and (iii) were used in a prior study (*5*). Each playback loop consisted of two recordings from the same individual, starting every 5 seconds (i.e. a 10 second loop). While in a prior study recordings were played back every 7 seconds (i.e. a 14 second loop) (*5*), this shorter interval was chosen to better match Hadza signals, which are normally given at shorter intervals than Yao signals. Yao signals and control sounds were naturally similar in length (Yao signals: mean ±SE = 1.66 ±0.07 sec, range 1.18–2.60 sec; control sounds: mean ±SE = 1.60 ±0.05 sec, range 1.23–2.30 sec; data are mean lengths of the two recordings per person), whereas naturally given Hadza whistles are typically given in a long series resulting in a signal of greater and more variable length (up to several minutes in duration). We therefore extracted clips of sequences of Hadza whistles (containing several whole notes) of a similar length to the other two treatments (mean ±SE = 1.49 ±0.07 sec, range 1.05–2.62 sec). This should render our findings conservative, since honeyguides were exposed only to a subset of the typical Hadza whistle sequence with which the Tanzanian honeyguide study population was familiar. Playback sound lengths did not significantly differ across the three treatment types ($R^2 = 0.07$, $F_{2,74} = 2.68$, $p = 0.075$; playback lengths log-transformed to improve normality of residuals). During trials, as we walked we rotated the orientation of the speaker between playbacks (left; forward; right; forward, etc.) to approximate omnidirectional human signals.

Measurement of sound attenuation

To compare attenuation of different experimental playback types in the physical environmental of our study sites, we played back the same recordings in an area of typical habitat on a wind-free day in each of our study sites at the same time as the experiments (on 25–26 July 2017 in Tanzania and 19–20 December 2016 in Mozambique), such that leaf and grass cover was similar. We rotated the sequence of playback exemplars between the three treatments types in blocks of four, to avoid any bias from weather conditions. We recorded amplitude at 3 m and 30 m using the NTi XL2 sound level meter and acoustic analyser. This logs amplitude at 0.1 second intervals alongside a WAV file of the measured sound. To calculate amplitudes over the duration of each sound, we manually extracted the series of measurements associated with each syllable or note (that is, excluding the gaps between syllables/notes, defined as measurements less than 45 dBA at 3 m, which excluded background sounds such as bird calls in the environment), following (*5*). Because the instrument logs measurements at 0.1 second intervals, minor variation in the synchronisation of sound and logging intervals generates minor variation in recorded amplitudes. We therefore calculated amplitude for two replicates of each sound, and analysed the mean of two sounds per individual. Attenuation was then calculated as the linear decrease in amplitude between measurements at 3 m and at 30 m. We calculated this measure for both maximum amplitude, and mean amplitude over the duration of the sound (excluding gaps as defined above).

Acoustic analysis of playback exemplars

For our control treatment, we alternated playbacks of Yao and Hadza voices at both sites; thus, the experimental design guarded against any potential familiarity of honeyguides to local versus foreign voices. Nonetheless, as a precaution, we checked whether the control treatments of Yao origin differed acoustically from those of Hadza origin, and whether control treatments of each origin differed in their degree of similarity with the two honey-hunting signal types (Yao trill-grunts and Hadza whistles).

To do so we used the R package warbleR (*50*) to acoustically analyse the playback exemplars we used in the field experiments. First we used the function autodetect to extract sound elements from the playback exemplar WAV files (88 elements from the 26 Yao signal exemplars, 110 elements from the 27 Hadza signal exemplars, 53 elements from the 12 control exemplars of Yao origin, and 60 elements from 12 control exemplars of Hadza origin). We then used the function spectro_analysis to extract 27 acoustic parameters from each element, including various metrics of sound duration, frequency, and energy distribution (listed in Table S3). Some of these parameters were highly correlated with one another and therefore redundant. For each subset of the data analysed, we generated a correlation matrix and arbitrarily discarded one of each pair of parameters that were highly correlated ($r > 0.75$). Table S3 indicates which parameters were retained for each analysis. For each subset of the data analysed, we then used a principal components analysis to extract and plot two main axes of variation in these parameters (variation explained by PC1 and PC2 given on plot axes).

The PCA plots show acoustic parameters of Yao voices and Hadza voices giving control sounds overlapped widely (Fig S1). Acoustic parameters of Yao voices and Hadza voices giving control sounds also overlapped widely with Yao honey-hunting signals (Fig S2). This implies that the trend for an elevated response by Mozambican honeyguides to control sounds compared to Tanzanian honeyguides cannot be explained by Yao control sounds being more similar than Hadza control sounds to Yao honey-hunting signals (and so leading to an elevated response to the subset of controls that were of Yao origin). By contrast, and as expected given the contrast between vocal sounds and whistles, acoustic parameters of all vocal sounds (Yao honey-hunting signals, and control sounds of both Yao and Hadza origin) were similar to one another and largely non-overlapping with those of Hadza honey-hunting signals (Fig S3).

Statistical analyses

We used R version 4.2.1.(*51*) for all statistical analyses. We analysed experimental data using logistic regression models with a logit link function, and used planned comparisons to assess differences between the three treatment levels, as recommended by ref (*30*) since the hypothesis a priori predicted specific differences between treatments. We checked model assumptions and calculated percentage of variance explained (R^2) following ref (*52*). Following ref (*5*), in addition to experimental treatment, we modelled additional covariates designed to take into account any diurnal variation in honeyguide activity: start time of the trial, measured in hours from sunrise or to sunset; air temperature at the end of the trial; and morning vs afternoon, since honeyguide activity may vary between the two for reasons independent of time to sunrise/sunset and temperature (e.g. hunger). When added as predictor variables into our logistic regression analyses, none of these variables lowered model AIC values, and thus we do not report those analyses. We analysed differences in sound attenuation between sound types and countries using ANOVA, and implemented post-hoc tests using the R package agricolae (*53*).

In addition to the planned comparisons of guiding rates reported in the main text (Fig. 1), and after viewing the staggered distribution of guiding probabilities across the three acoustic conditions at Niassa (Fig 1C), we also carried out an exploratory post-hoc analyses comparing guiding rates across all three acoustic treatments in Mozambique, using logistic regression. The model-estimated log odds for guiding under the reference condition of a Yao call was 0.9985. When a human voice control sound was played back, the log odds of a honeyguide responding decreased by -0.9985 ($p = 0.097$). When a Hadza whistle was played back, the log odds decreased by -2.0484 ($p = 0.001$). This suggests that in Mozambique, a decrease in honeyguide response rates was observed whenever sounds other than the Yao trill-grunt were played back, and that these lower response rates each contributed to the result reported in the main text (Fig

1). However, the difference in log odds was greater when the Hadza whistle was played back, and thus, this condition seems to more strongly drive the result of our planned comparison than did the lowered honeyguide response rate in relation to the human voice control sounds.

A greater degree of acoustic similarity between the human voice control sounds and the Yao trill-grunt call, relative to the Hadza whistles (Fig. S3), could perhaps generate greater similarity in guiding rates in Mozambique between the local (Yao) call and the human control sounds, as compared to in Tanzania, where the difference in honeyguide responses between the local (Hadza) call and control voices appears to be larger (cf. Fig. 1B vs. 1C). Alternatively, it could be that human voices are a semi-reliable cue to the presence of a honey-hunter in Mozambique, because most people in the Niassa Special Reserve are likely to interested in honey-hunting, and thus, control human voices frequently attract honeyguides. In Tanzania, by contrast, Datoga pastoralists share the landscape with Hadza people, and since this population does not honey-hunt, this makes human voices, in general, a less reliable cue to the presence of a honey-hunter. Our study was not designed to test these hypotheses, but our exploratory analyses and qualitative observations suggest these directions for future research.

Strategic models of human-honeyguide communication

Here we present two formal models of human-honeyguide communication. Our first model shows how the mutual benefits of the cooperative partnership should produce local signaling traditions. Our second model shows how human cultural variation influences the utility of different kinds of signals that can be used to attract honeyguides.

Model 1: Within regions, a coordination game generates local traditions of inter-species communication

Here we consider the signal choices of honeyguides and honey-hunters, in the form of a two-player game. In this model, we simply assume that if a honey-hunter and a honeyguide cooperate, they each receive the benefits of the mutualism, and earn a payoff M. If they fail to cooperate, we assume they earn the payoff of a lone forager, L, and that $L < M$. The payoff matrix in Table S4 represents these incentives, and considers a honey-hunter's decision of whether to produce signal A or an alternative form, signal B. Similarly, a honeyguide must decide whether to respond to signal A or B. Under these conditions, a coordination game (*33*) arises.

Our experimental results show that honeyguides can learn to associate a range of signals with the presence of a honey-hunter. However, as with human language, the local use of shared signals creates opportunities for mutual understanding, coordination, and beneficial interactions. In this coordination game, each partner maximizes their benefits if the same signal is produced and responded to. There are two evolutionarily stable strategies (*54*) in this coordination game: honey-hunters signalling A and honeyguides responding to A, or honey-hunters signalling B and honeyguides responding to B. Once either of these local communicative traditions is established, any individuals that decided to produce or respond to a different signal would receive a lower payoff (L), and as a result, such strategies would not be able to invade the population. Our experimental results attest to this feature. A Yao honey-hunter who decided to use Hadza whistles in the Niassa Special Reserve (simulated by our playback experiments) would not attract many honeyguides, and nor would a Hadza honey-hunter who decided to use Yao trill-grunts in the Kidero Hills (Fig. 1, Fig 3). This should lead to the formation of local signalling traditions, in which new generations of honey-hunters are incentivized to produce the signals that local honeyguides already respond to, and likewise, new generations of honeyguides are incentivized to respond to the signals that local honey-hunters already produce. Once a convention (i.e. a solution to a coordination game) has been established, it pays to learn it.

Model 2: Among regions, cultural variation and economic trade-offs structure the value of signals

Here we show how ecological and cultural variation can impact the fitness value of different signals used for coordination. Modeled on Hadza-Yao cultural differences, we consider how one feature of a honeyguide-attracting signal – how conspicuous it is to mammals – can structure signal value across cultural regions. As noted in the main text, members of the Hadza community are simultaneously interested in locating sources of wild honey and pursuing mammals that they may encounter on the landscape. In contrast, the Yao people do not hunt wild mammals during honey-hunting forays. Hunting has been forbidden in the Niassa Special Reserve since its establishment in the 1950s, and prior to that, hunting was conducted primarily via snares and pitfall traps rather than stealth hunting. The contrast between the Yao and the Hadza in this regard reflects their divergent cultural histories and descent from Bantu-speaking farmers and Hadzane-speaking hunter-gatherers, respectively. Importantly, the logic of this model applies regardless of whether the importance of mammal hunting is wholly owing to the vertical cultural transmission of subsistence practices or other factors.

In this model, we assume that foragers are seeking to maximize their rates of energy capture (E_T, kcal / hour), and that rates are determined by the efficiencies of hunting mammals (E_M) and hunting honey (E_H) and the proportion of time spent in each activity (P_M, P_H, with $P_M + P_H = 1$).

$$E_T = E_M + E_H \qquad (1)$$

We also assume that signals used to attract honeyguides vary in their conspicuousness (C). We assume that highly conspicuous signals increase encounter rates with honeyguides, thus increasing returns from honey-hunting. We also assume that signal conspicuousness has a negative effect on mammal hunting return rates, because more conspicuousness signals will scare away potential prey animals. The magnitude of the negative effect of signal conspicuousness on mammal hunting is determined by the variable M_M, and the magnitude of the positive effect of signal conspicuousness on honey-hunting is represented by variable M_H. Our model assumes that the efficiency of mammal hunting (E_M) is a function of its "baseline profitability", β_M, the proportion of time spent mammal hunting, P_M, and the negative effect of the conspicuousness of honeyguide-attracting signals ($1-M_M*C$).

$$E_M = P_M * \beta_M * (1-M_M*C) \qquad (2)$$

Likewise, the efficiency of honey-hunting (E_H) is a function of its baseline profitability, β_H, the proportion of time spent honey-hunting, P_H, the conspicuousness of honeyguide-attracting signals, C, and the positive effect of signal conspicuousness on honey-hunting, M_H.

$$E_H = P_H * \beta_H * (1+M_H*C) \quad (3)$$

Substituting (2) and (3) into (1), we have

$$E_T = P_M * \beta_M * (1-M_M*C) + P_H * \beta_H * (1+M_H*C) \quad (4)$$

Using equation (4), we first ask: under what conditions does increasing the conspicuousness of signals, C, increase rates of energy capture? Increasing the conspicuousness of signals will increase the total energy capture rate when the increased efficiency in honey-hunting more than compensates for the decrease in efficiency in mammal hunting. For an increase in C to increase E_T, it must be true that:

$$P_H * \beta_H * (1+M_H*C) - P_M * \beta_M * (1-M_M*C) > 0 \quad (5)$$

Under what conditions is (5) true? The first condition under which this is true, Scenario 1, is if $P_M = 0$. Assuming such, inequality (5) simplifies to

$$P_H * \beta_H * (1+M_H*C) > 0 \quad (6)$$

Which is true whenever a non-zero amount of time is spent honey-hunting ($P_H > 0$) and the rate of energy capture from honey-hunting is greater than zero ($\beta_H > 0$). That is, if foragers spend none of their time hunting mammals, more conspicuous signals will increase total foraging return rates. This condition is met in the case of the Yao, who do not hunt mammals during honey-hunting forays. More generally, by taking the derivative of (4) with respect to C, we know that an increase in conspicuousness (C) will increase total energy capture (ET) whenever:

$$P_H * \beta_H * M_H > P_M * \beta_M * M_M \quad (7)$$

If we consider another case (Scenario 2) in which foragers equally divide their time between hunting mammals and hunting honey (i.e. $P_H = P_M = 0.5$), and where the magnitude of the effect of conspicuousness is equal in both contexts ($M_H = M_M$), then inequality (7) would simplify to

$$\beta_H > \beta_M \quad (8)$$

In Scenario 2, increasing conspicuousness would also increase energy efficiency as long as the baseline profitability of honey hunting is greater than that of mammal hunting. Now we may consider Scenario 3, a group of foragers in a cultural and environmental context where mammal hunting is twice as profitable as honey hunting ($\beta_M = 2 * \beta_H$) who spend twice as much time mammal hunting as honey hunting ($P_H = 0.33$, $P_M = 0.66$). In this scenario, inequality (7) becomes:

$$0.33 * \beta_H * M_H > 0.66 * 2 * \beta_H * M_M \quad (9)$$

Simplifying,

$$0.33 * M_H > 1.32 * M_M \qquad (10)$$

For such foragers, an increase in signal conspicuousness is less likely to be profitable (i.e. increase E_T) because the positive effect of signal conspicuousness on honey hunting must be greater than 4 times its negative effect on mammal hunting. For example, a more conspicuous signal that increased the profitability of honey hunting by 50% ($M_H = 0.5$) would not be advantageous to use unless its negative effect on mammal hunting was quite slight, and decreased hunting incomes by less than 12.5%. This asymmetry would become more extreme, under scenarios of increasing profitability and commitments to mammal hunting.

This model formalizes the logic of our argument about how ecological and cultural differences influence the value of honeyguide-attracting signals. Together, the three modelled scenarios show that 1) under conditions where mammal hunting is restricted or otherwise not pursued, such as in the case of the Yao, increases in signal conspicuousness should generally increase energy capture rates; 2) that when mammal hunting and honey-hunting are equally pursued, the net effect of increasing signal conspicuousness depends on the relative profitability of pursuing mammals or honey and the effect of signals upon both; and that 3) in contexts where mammal hunting is more profitable and more committed to than honey hunting, signal conspicuousness will be limited, even if more conspicuousness signals appreciably increase potential honey hunting incomes. More qualitatively, these models suggest that there should generally be a negative association between the importance of mammal hunting and the conspicuousness of honeyguide-attracting signals, in terms of their propensity to alert wary prey mammals. This model could also be extended to generate predictions about the conspicuousness of honeyguide-attracting signals employed within one cultural region, across spatial gradients of mammal density, across individuals of varying abilities, or across time as seasonal or more long-term changes structure the profitability of pursuing mammals vs. honey.

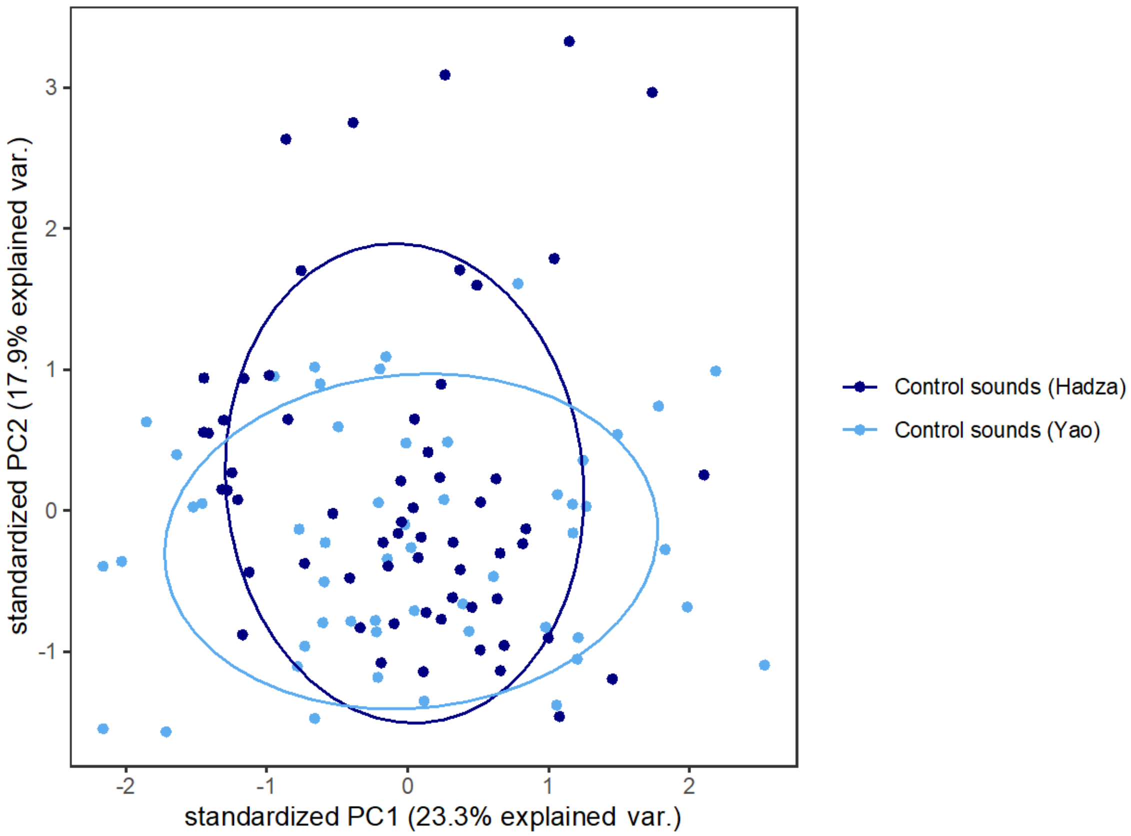

Fig. S1. Principal components analysis of 12 acoustic parameters (listed in Table S3) extracted from playback exemplars used in the field experiments, including only the control treatment: control sounds of Hadza (dark blue) and Yao (pale blue) origin.

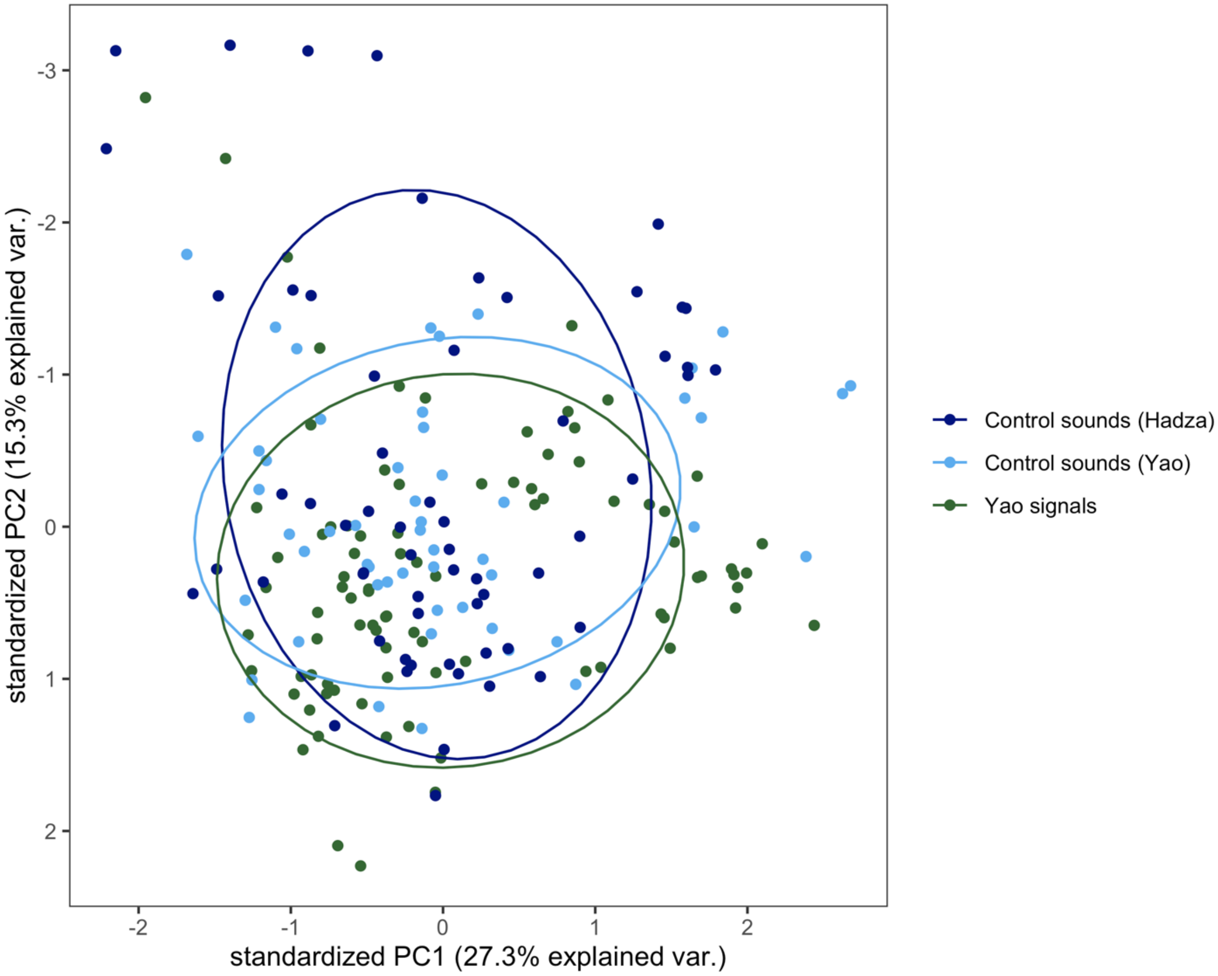

Fig. S2. Principal components analysis of 13 acoustic parameters (listed in Table S3) extracted from playback exemplars used in the field experiments, including all treatments involving human vocal sounds: Yao honey-hunting signals (green), and control sounds of Hadza (dark blue) and Yao (pale blue) origin.

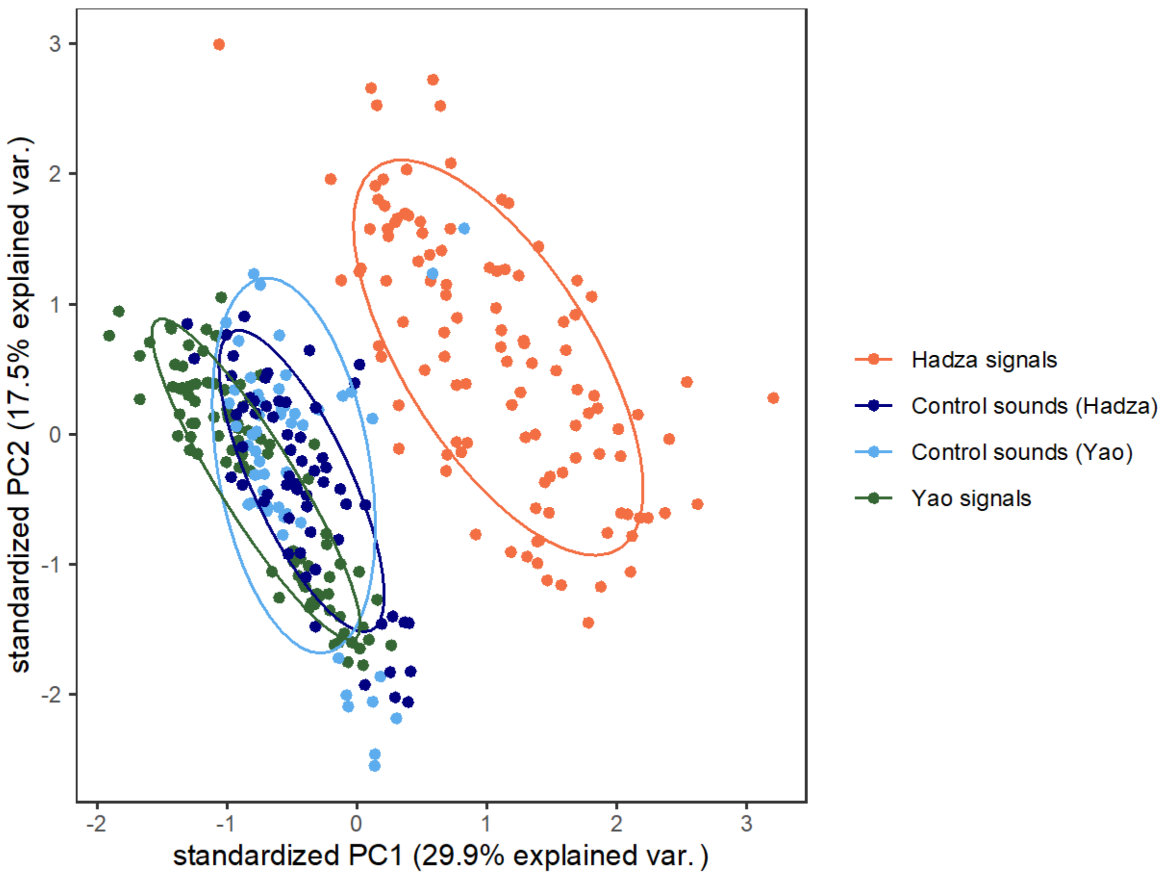

Fig. S3. Principal components analysis of 14 acoustic parameters (listed in Table S3) extracted from playback exemplars used in the field experiments, including all treatment types: Yao honey-hunting signals (green), Hadza honey-hunting signals (orange), and control sounds of Hadza (dark blue) and Yao (pale blue) origin.

Table S1. Attenuation rate of different sound types (exemplars used in playback experiments: Hadza signals, Yao signals, and human control sounds) at each experimental location (country: Tanzania vs Mozambique). Maximum amplitude of all sound types attenuated less in Tanzania than in the more occluded habitat of Mozambique. Post-hoc tests (Scheffe's test) indicated that Hadza signals attenuated less than both other sound types with respect to both maximum amplitude ($p < 0.001$), and less than Yao signals with respect to mean amplitude ($p = 0.039$). However, there are no statistically significant country by sound type interactions, indicating that all three sounds attenuated similarly in both environments. Model adjusted R^2 are 0.195 and 0.023 for maximum and mean amplitude respectively.

	df	*F*	*p*
Attenuation of maximum amplitude:			
country	1	6.81	0.010
sound type	2	17.52	< 0.001
country * sound type	2	0.11	0.896
Attenuation of mean amplitude:			
country	1	0.00	0.966
sound type	2	3.78	0.025
country * sound type	2	0.51	0.602

Table S2. Logistic regression models including the attenuation rates of each playback exemplar (when played in the relevant environment) as a predictor variable. Attenuation rate of neither maximum amplitude nor mean amplitude explains any additional variation in honeyguide responses to experimentally played sounds.

	estimate ±SE	*Z*	*P*
Experiment in Tanzania:			
local signal vs. foreign signal and control sounds	1.67 ±0.44	3.77	<0.001
foreign signal vs. control sounds	-0.07 ±0.34	-0.22	0.827
attenuation of maximum amplitude	-0.05 ±0.19	-0.27	0.787
ΔAIC compared to model reported in main text = 1.93			
local signal vs. foreign signal and control sounds	1.64 ±0.41	4.02	<0.001
foreign signal vs. control sounds	-0.05 ±0.33	-0.16	0.870
attenuation of mean amplitude	-0.16 ±0.22	-0.73	0.467
ΔAIC compared to model reported in main text = 1.46			
Experiment in Mozambique:			
local signal vs. foreign signal and control sounds	1.07 ±0.36	2.94	0.003
foreign signal vs. control sounds	-0.67 ±0.34	-1.96	0.050
attenuation of maximum amplitude	-0.12 ±0.13	-0.97	0.332
ΔAIC compared to model reported in main text = 1.03			
local signal vs. foreign signal and control sounds	1.05 ±0.36	2.90	0.004
foreign signal vs. control sounds	-0.55 ±0.31	-1.81	0.070
attenuation of mean amplitude	-0.12 ±0.17	-0.72	0.474
ΔAIC compared to model reported in main text = 1.48			

Table S3. Acoustic parameters extracted by the R package warbleR (*48*). Parameters included in principal components analyses of three subsets of the data are indicated with an X. Omitted parameters were highly correlated ($r \geq 0.75$) with other parameters in each subset of the data; for each highly correlated pair, the first parameter on the list was arbitrarily retained.

Measure	Description (reproduced from (*48*))	Control sounds only	Control sounds and Yao signals	All sound types
duration	length of signal (in s)	X	X	X
meanfreq	mean frequency (in kHz). Calculated as the weighted average of the frequency spectrum (i.e. weighted by the amplitude within the supplied band pass)	X	X	X
sd	standard deviation of frequency (in kHz). Calculated as the weighted standard deviation of the frequency spectrum			X
freq.median	median frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of equal energy (in kHz)			
freq.Q25	first quartile frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of 25% and 75% energy respectively (in kHz)	X	X	X
freq.Q75	third quartile frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of 75% and 25% energy respectively (in kHz)			
freq.IQR	interquartile frequency range. Frequency range between 'freq.Q25' and 'freq.Q75'			
time.median	median time. The time at which the time envelope is divided in two time intervals of equal energy (in s)			
time.Q25	first quartile time. The time at which the time envelope is divided in two time intervals of 25% and 75% energy respectively (in s).	X	X	X
time.Q75	third quartile time. The time at which the time envelope is divided in two time intervals of 75% and 25% energy respectively (in s)			
time.IQR	interquartile time range. Time range between 'time.Q25' and 'time.Q75' (in s)			
skew	skewness. Asymmetry of the frequency spectrum	X	X	X
kurt	kurtosis. Peakedness of the frequency spectrum			

sp.ent	spectral entropy. Energy distribution of the frequency spectrum. Pure tone ~ 0; noisy ~ 1.		X	X
time.ent	time entropy. Energy distribution on the time envelope. ~0 means amplitude concentrated in a specific time point, 1 means amplitude equally distributed across time		X	X
entropy	spectrographic entropy. Product of time and spectral entropy sp.ent * time.ent			
sfm	spectral flatness. Similar to sp.ent (Pure tone ~ 0; noisy ~ 1)			
meandom	average of dominant frequency measured across the spectrogram	X	X	
mindom	minimum of dominant frequency measured across the spectrogram	X	X	X
maxdom	maximum of dominant frequency measure across the spectrogram			X
dfrange	range of dominant frequency measured across the spectrogram			
modindx	modulation index. Calculated as the cumulative absolute difference between adjacent measurements of dominant frequencies divided by the dominant frequency range (measured on the spectrogram)	X		X
startdom	dominant frequency measurement at the start of the signal (measured on the spectrogram)	X	X	X
enddom	dominant frequency measurement at the end of the signal (measured on the spectrogram)	X	X	X
dfslope	slope of the change in dominant frequency (measured on the spectrogram) through time			X
peakf	peak frequency. Frequency with the highest energy and is measured on the frequency spectrum	X	X	
meanpeakf	mean peak frequency. Frequency with highest energy from the mean frequency spectrum	X	X	

Table S4. Coordination game of signal choice. Owing to mutualism, a honey-hunter and a honeyguide who coordinate on a signal earn *M*, a value that is greater than *L*, which is received by those who fail to collaborate and forage alone (see description of model 1 for details).

		Honey-hunter (HH) payoff	
		Produce signal A	Produce signal B
Honeyguide (HG) payoff	Respond to signal A	M_{HH}, M_{HG}	L_{HH}, L_{HG}
	Respond to signal B	L_{HH}, L_{HG}	M_{HH}, M_{HG}

Captions for Audio S1 to S2

Audio S1. Examples of natural communication between greater honeyguides and honey-hunters to coordinate cooperation, as bird and human move together towards a bees' nest (i.e. after cooperation has successfully been initiated). From 0 sec, Maogola Mdungai, a Hadza honey-hunter, calls to a guiding honeyguide (an adult female) in the Kidero Hills, Tanzania, on 17 July 2017; from 20 sec, Seliano Rucunua, a Yao honey-hunter, calls to a guiding honeyguide (an adult male) in the Niassa Special Reserve, Mozambique, on 10 September 2022.

Audio S2. Representative exemplars of sounds used in the playback experiments: one set of two sounds for each treatment (Hadza honey-hunting signal, Yao honey-hunting signal, and human control sounds), at 5 s intervals as used in playbacks. Calls are given respectively by Hadza honey-hunter Marikizadeki Mwengera, Yao honey-hunter Issofu Kambunga, and Hadza Honey-hunter Kaunda Hassani.

Captions for Movies S1 to S2

Movie S1. Msa Sapo, a Hadza hunter, describes why whistles are a good way to communicate when hunting.

Movie S2. Kaunda Ndofu, a Hadza hunter, describes why whistles are a good way to communicate when hunting.

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