

Title: Culturally-determined interspecies communication between humans and honeyguides

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Abstract: 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.

One-Sentence Summary: Honeyguide birds understand culturally varying signals used by human honey-hunters, leading to different cultures of interspecies cooperation.

Main Text: 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 geographically vary (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 unrivalled capacity for social learning (7). Our species' cultural adaptability has allowed us to invade novel environments and dominate landscapes (8), and produces diverse behavioural responses in wild non-human 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, 10). 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 making us highly efficient honeyguide partners (10). 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, striking cultural variability exists in the traits that mediate it, including how people attract honeyguides. Honey-hunters often use specialised 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 from the Hadza (also known as Hadzabe) cultural 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 (10, 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'll find less honey (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 based on variable interactions with people (23). A priori, we expect that preferences for specific human signals would be learned by honeyguides, rather than arise through 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 (10)) 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 minutes each) and in the Kidero Hills of northern Tanzania ($N = 75$ transects of 30 minutes each; longer transects 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, 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 $\pm$ 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 $\pm$ 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 $\pm$ 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 towards 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, since 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 least, but all sounds attenuated similarly across environments (Fig. 2; Table S1). Therefore, honeyguides were not more likely to hear local signals given in their local habitat. Second, models including 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, 10, 16, 21, 22), including within 100 km of our study sites (20). We suggest that these differences may not always be arbitrary, since 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 unique cultural heritage and genetic descent from hunter-gatherers who lived in the region prior to the arrival of herders and farmers over the last 4,000 years (34-36). The main economic pursuits of Hadza men are collecting wild honey and hunting animals (36, 37). While honey-hunting, Hadza 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 which fear human voices (39). In interviews carried out between 2015–2021, 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 recognisably human, as confirmed by acoustic analysis (Figs. S2–S3). A non-mutually 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 who use whistled speech to 1) evade detection by game animals and prevent eavesdropping by outsiders, and 2) 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 non-significant 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 modelling 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, 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 behaviour 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 via 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 since 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 favouring 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 non-human 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 stabilise mutualisms, by facilitating choice of cooperative partners (2). Cultural traditions of consistent behavior are widespread in non-human animals (3) and could plausibly mediate other

forms of interspecies cooperation. Reciprocal phenotypic plasticity via 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

Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S4

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References (49–54)

Audio S1 to S2

Movies S1 to S2

Figures and Figure Legends

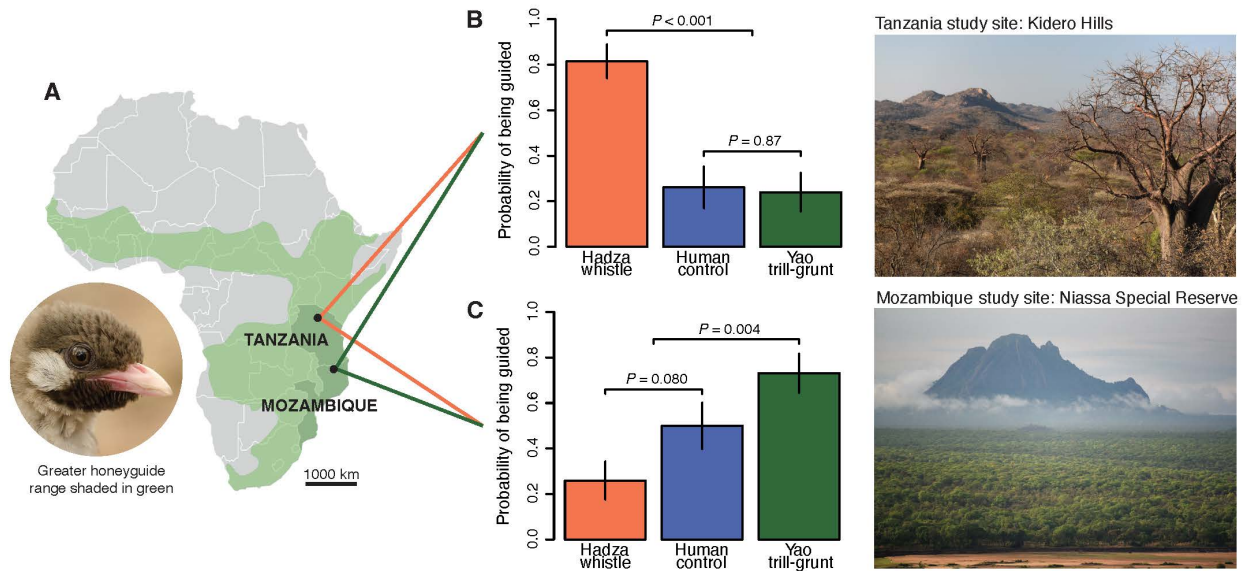


Fig. 1. Honeyguide cooperative behaviour in response to experimental acoustic playbacks. We carried out the same experimental treatments at (A), Kidero Hills inhabited by Hadza people in Tanzania and Niassa Special Reserve inhabited by Yao people in Mozambique. Values are probabilities of honeyguides 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.

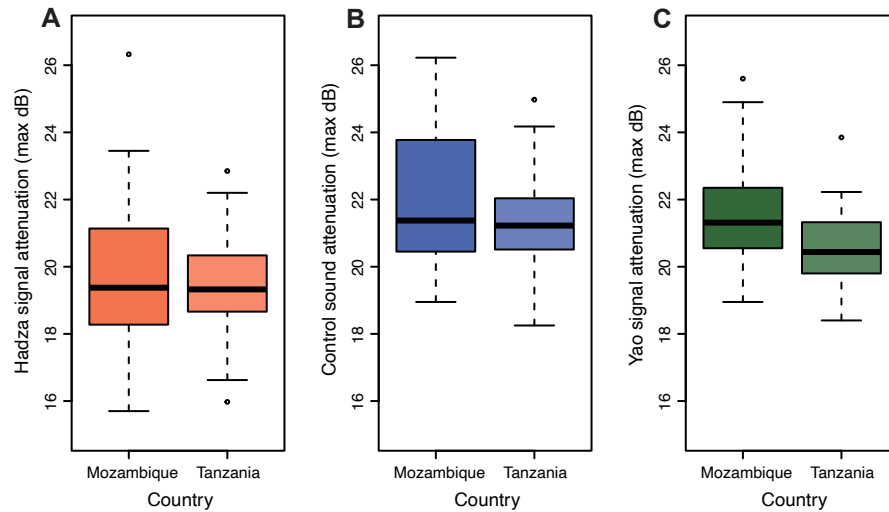


Fig. 2. Acoustic attenuation of honey-hunting signals used by different human cultures, and controls. (A), whistles used by Hadza people in Tanzania, (B), arbitrary human sounds and (C), trill-grunts used by Yao people in Mozambique all attenuate similarly from 3 m to 30 m distance in their local environment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

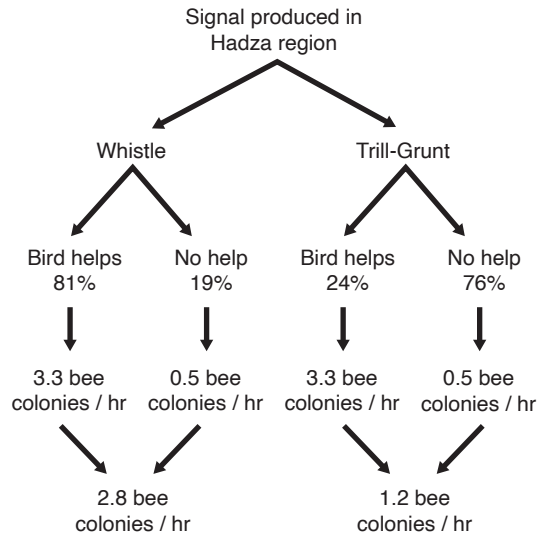


Fig. 3. The expected payoffs to whistling or trill-grunting in the Hadza region. Probabilities of guiding are taken from this study (Fig. 1). In a prior study, Hadza honey-hunters found bees' nests at a rate of 3.3 / hour when helped by honeyguides, and 0.5 / hour without their help (16). A honey-hunter in the Hadza region who committed to whistling to attract honeyguides for 30 minutes would be expected to find bees' nests at a rate of 2.8 / hour ($0.81 * 3.3 + 0.19 * 0.5$), while one who trill-grunted would realize a rate of 1.2 / 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).