Title: Honeyguides Prefer To Lead Humans Who Signal That They Will Follow

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Abstract: Greater honeyguides (*Indicator indicator*) lead human honey-hunters to wild bees' nests, in a rare example of a mutualistic foraging partnership between humans and free-living wild animals. We show experimentally that a specialized vocal sound made by Mozambican honey-hunters seeking bees' nests elicits elevated cooperative behavior from honeyguides. The production of this sound increased the probability of being guided by a honeyguide from about 33% to 66%, and the overall probability of thus finding a bees’ nest from 17% to 54%, as compared to other animal or human sounds of similar amplitude. These results provide experimental evidence that a wild animal in a natural setting responds adaptively to a human signal of cooperation.

Main Text: In 1588, a Portuguese missionary in Sofala (in present-day Mozambique), João dos Santos, often noticed a small bird flying through cracks in the walls of his mission church and nibbling wax from the candlesticks within. This kind of bird, he wrote, had another peculiar habit, of leading men to bees' nests by calling and flying from tree to tree. After the men harvested the honey, the bird would eat the wax combs left behind (*1*). We now know this species to have been the greater honeyguide, and dos Santos's description to have been accurate. Honeyguides eat beeswax and know where bees' nests are located; humans can subdue the bees and open the nest using fire and tools, thus exposing beeswax for the honeyguides and honey for the humans (*2*). This interaction remains an extremely rare example of mutualism between free-living wild animals and our own species. Here, we show that it is also a unique example of reciprocal communication between birds and humans.

Greater honeyguides (Figure 1a) seeking a human collaborator approach people and give a loud chattering call (Audio S1). This call is distinct from their territorial song and is accompanied by referential gestures (*3*): the bird flies from tree to tree in the direction of the bees' nest, until its human follower finds the bees' nest (*2, 4*). The honeyguide thus directs a signal of the bees' nest location towards humans, which honey-hunters use to mutual advantage. In this study, we ask whether honeyguides in turn exploit specialized signals directed at them by humans. We studied greater honeyguides (hereafter "honeyguides") in the Niassa National Reserve in northern Mozambique. This region has been noted for its honey and beeswax production at least since Arab trading times centuries ago (*5, 6*). The local Yao people still harvest wild honey using traditional methods, and this practice remains economically important.

First we confirmed that in northern Mozambique, honeyguides give reliable information to human honey-hunters. To test whether guiding behavior accurately indicates the direction of bees' nests and leads to their successful discovery by humans, we followed honey-hunters following honeyguides and tracked our movements with a GPS. A guiding event was defined as a bout of guiding by an individual bird, sometimes involving consecutive journeys to different bees' nests. Each guiding event probably involved a different individual honeyguide as the study area was 230 km^2, and the home-ranges of individual honeyguides that we measured using radio telemetry did not exceed 1 km^2 and overlapped with one another (*7*) (Figure S1). 75.3% of guiding events led to the successful discovery by humans of at least one bees' nest (mean ±SE = 1.00 ±0.08, range 0–3 nests; n = 97 events excluding controls in experiment below (*7*)). 94.6% of nests shown belonged to the honeybee *Apis mellifera*, and the rest to stingless bee species (*7*). Nests were located 0–832 m (median = 152 m, *n* = 84 nests, only considering the first nest per guiding event) from the point where guiding began. Figure 1b shows that the birds' initial flight direction accurately signaled the ultimate location of the bees' nest, corroborating a classic study from Kenya (*2*). Overall, 74.5% of bees' nests found by humans (*n* = 149) involved the help a honeyguide.

Second, we asked whether the signals used by human honey-hunters provide reliable information to honeyguides. Honey-hunters seeking honeyguides often announce their presence with unspecialized sounds such as shouting and chopping wood (*4, 8*). In some parts of Africa, however, humans also use specialized sounds only given when hunting honey: in the Niassa National Reserve (and more widely in northern Mozambique and adjacent southern Tanzania), Yao honey-hunters seeking and following honeyguides produce a loud trill followed by a grunt: "brrrr-hm" (Audio File S1; see (*9*) for a melodious whistle used in the same context by the Hadza people of northern Tanzania). To confirm that "brrrr-hm" is a specialized honey-hunting sound, we interviewed 20 Yao honey-hunters, all of whom reported that they used this specific sound when hunting honey, and in no other context. When asked why, they reported that they learnt it from their fathers, and that it is the best way of attracting a honeyguide. Therefore, this sound has the potential to reliably signal to honeyguides that a prospective human partner is specifically seeking honey and has the tools, skills and time to open a bees' nest, which many humans do not. A payoff to the bird reliably results from interacting with such a partner, because if a bees' nest is harvested then wax is left behind either as combs containing no honey, or as chewed lumps spat out by honey-hunters.

Finally, we asked whether honeyguides associated this signal with a higher chance of a payoff from cooperation. If so, then honeyguides should be more likely to initiate collaboration with humans producing this honey-hunting sound rather than other sounds. To test this we carried out 72 fifteen-minute experimental transects simulating honey-hunting forays, in which an author and two local honey-hunters walked while playing back one of three acoustic cues every seven seconds at consistent amplitude using a calibrated speaker: (i) a control human sound (the Yao words for "honeyguide…honey" or the honey-hunter's name, alternated among transects); (ii) a control animal sound (the song or the excitement call of the ring-necked dove, *Streptopelia capicola*, alternated among transects); or (iii) the specialized "brrrr-hm" honey-hunting sound (see (*7*) for details and Audio Files S2–S4 for examples). Each transect used a unique playback exemplar recorded from a different individual person or bird. Honeyguides have never been confirmed to guide any species besides humans (*10*). We conducted this experiment during the hot dry season and shade air temperatures at the end of each transect were on average 31ºC (range 23–38ºC). Therefore, we also tested the effects of temperature, trial time relative to sunrise/set, and morning vs. afternoon (details in (*7*)).

We were guided by a honeyguide on 30 of 72 transects. Transects accompanied by the honey-hunting call had a 66.7% probability of eliciting guiding from a honeyguide, which was significantly greater than that on transects accompanied by the human control sounds (25%) or animal control sounds (33.3%) (Figure 2a; planned comparison with controls: estimate ±SE = 1.13 ±0.38, $Z = 2.96$, $P = 0.0031$); the probability of guiding did not differ between the two control treatments (estimate ±SE = 0.25 ±0.33, $Z = 0.76$, $P = 0.45$). The best model also included the time relative to sunrise or sunset as a covariate (probability of being guided weakly decreased closer to the middle of the day: estimate ±SE = -4.34 ±0.20, $Z = -2.13$, $P = 0.034$), and overall explained 25% of the variance in probability of being guided by a honeyguide.

Once a honeyguide initiated guiding behavior, we followed it while continuing to play back the acoustic treatment, while the honey-hunters searched visually for bees' nests (see (*7*) for measures taken to encourage and validate equal search effort). This revealed that honeyguides tended to give up guiding behavior more often when the two control treatments were given, resulting in no bees' nests being found: of those transects on which we were guided by a honeyguide, we found a bees' nest on 81.3% of those accompanied by the honey-hunting sound, compared to 66.7% and 50.0% of those accompanied by the human and animal control sounds respectively. Overall, therefore, giving the honey-hunting sound resulted in a 54.2% predicted probability of finding a bees' nest (Figure 2b; planned comparison with controls: estimate ±SE = 1.21 ±0.39, $Z = 3.14$, $P = 0.0017$), compared to 16.7% when giving each of the control sounds (planned comparison between controls: estimate ±SE = 0.03 ±0.39, $Z = 0.08$, $P = 0.94$). Thus, the net effect of giving the honey-hunting sound was to more than triple the probability of finding a bees' nest during a standardized 15 minute search accompanied by an acoustic cue.

This experimentally validates the honey-hunters’ claims that the honey-hunting sound improves their foraging success.

Honeyguides might respond more to humans giving the honey-hunting sound either because they recognized and preferred it, or because they were simply more likely to hear it than control sounds. If the latter is true, then honeyguide behavior should be predicted by playback amplitude after attenuation in the environment. We measured the mean and maximum amplitudes (dBA) of every playback exemplar with a sound level meter at a distance of 30 m in the natural habitat (Table S1), and tested whether they explained any variance in guiding behavior either in isolation or in the multivariate models above. In no case did these acoustic measures explain any variance in the probability of being guided or being shown a bees’ nest (*7*). Therefore, the honeyguides' elevated response to the honey-hunting sound is unlikely to be explained by its audibility. Instead, the most parsimonious explanation is that honeyguides associate the honey-hunting sound with successful collaboration. Such partner choice should be adaptive by allowing honeyguides to improve their net benefit from interacting with humans.

These results show that a wild animal correctly attaches meaning and responds appropriately to a human signal of recruitment towards cooperative foraging, as previously known only from domestic animals such as dogs (*11*). Although humans use many species as foraging partners, including falcons, dogs and cormorants, these involve trained or domesticated individuals that are specifically taught to cooperate. The honeyguide-human relationship is remarkable in that it involves free-living wild animals whose interactions with humans have probably evolved through natural selection. To our knowledge the only comparable relationship involves cooperation between artisanal fishermen and free-living dolphins. Several reports exist of men “calling” dolphins to hunt, starting with Pliny the Elder ca. 70 AD (*12*). It remains unknown whether this reflects a similarly specialized communication system to that mediating the human-honeyguide mutualism in Mozambique.

How might honeyguides acquire information about honey-hunters' signals of cooperation? Honeyguides are brood-parasitic and reared by insectivorous hosts (*4*), suggesting that their propensity to locate bees' nests and guide humans to them are likely to be innate. However, the "brrrr-hm" human signal studied here is confined to a specific geographical area, and a different cultural group living 1000 km away uses a different signal which is likely to have the same function (*9*). Local adaptation is unlikely to account for corresponding honeyguide specialization, given a lack of obvious genetic structure across its range (*13*). This implies that local refinements to guiding behavior are probably learnt, supported anecdotally by the belief of Yao honey-hunters who often stated that juvenile honeyguides (which have distinctive yellow plumage (*4*)) are a separate species (called "namandindi") which, although it beckon humans in the manner of an adult honeyguide ("sego"), falls quiet in response to the honey-hunting sound. We propose that learning might occur socially from conspecifics in the vicinity of bees' nests, resulting in a local cultural tradition among honeyguides that reflects that of their human collaborators.

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Supplementary Materials

Materials and Methods
Table S1
Fig. S1
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Audio Files S1–S4

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Figure Legends

Fig. 1. **Greater honeyguides accurately guide humans to bees' nests.** (A) Yao honey-hunter and a wild, free-living honeyguide. (This bird has been captured using a researcher's mist-net and is neither tame nor habitually captive.) (B) Accuracy of honeyguide initial guiding behavior in relation to direction of successfully located bees' nests. Points represent the difference in bearing between initial guiding trajectory over the first 40 m of travel, and the ultimate direction of the bees' nest (here set at zero), and are binned into 5° intervals. Each point represents a journey (n = 58 journeys) to a separate bees' nest that was at least 80 m away from the point where guiding began; sometimes a honeyguide guided to more than one nest consecutively (n = 50 guiding events). The circular distribution is unimodal (Rayleigh test, $P < 0.001$) with a mean of 1.7º (95% confidence interval includes zero: 352.3º–11.1º), showing that honeyguide behaviour offers reliable directional information to humans.

Fig. 2. Probability of a successful mutualistic interaction, in relation to experimentally given acoustic cues. Values are predicted probabilities of (A) being guided by a honeyguide and (B) being shown a bees' nest on a 15 minute search, derived from a logistic model of data from experimental transects, and taking into account time of day (minutes from sunrise/to sunset). Boxes show medians and quartiles, and whiskers show ranges; n = 24 trials per treatment group; P-values show planned comparisons.

Figures

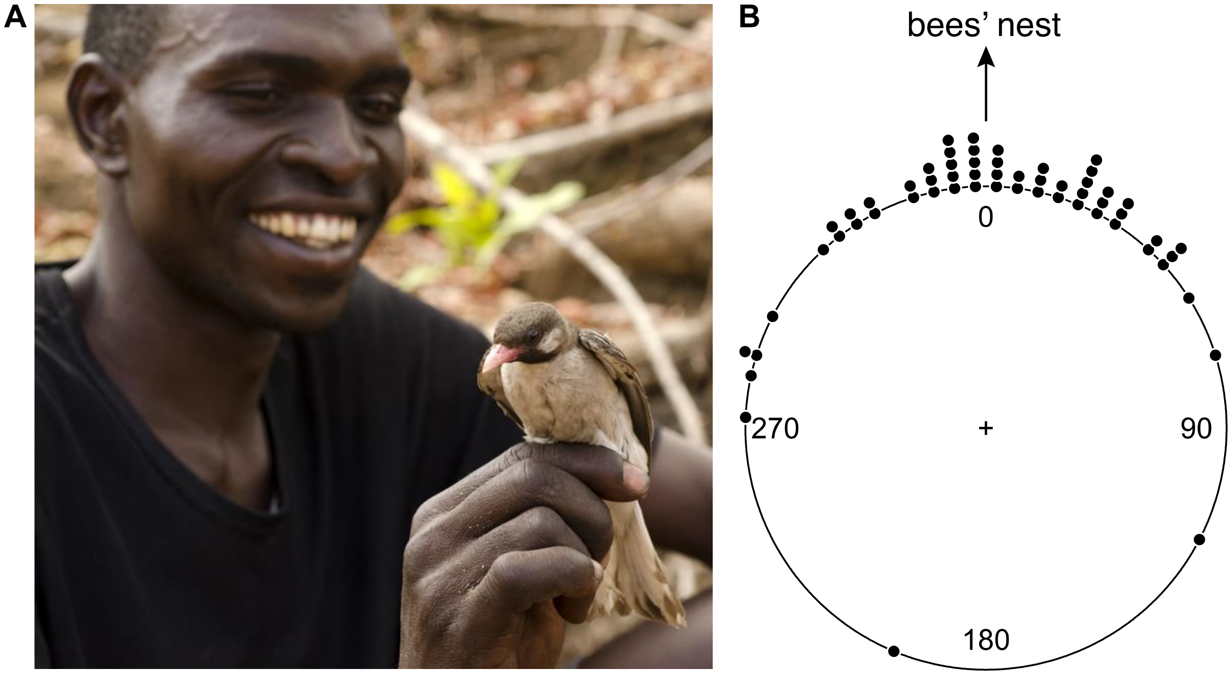

Fig 1.

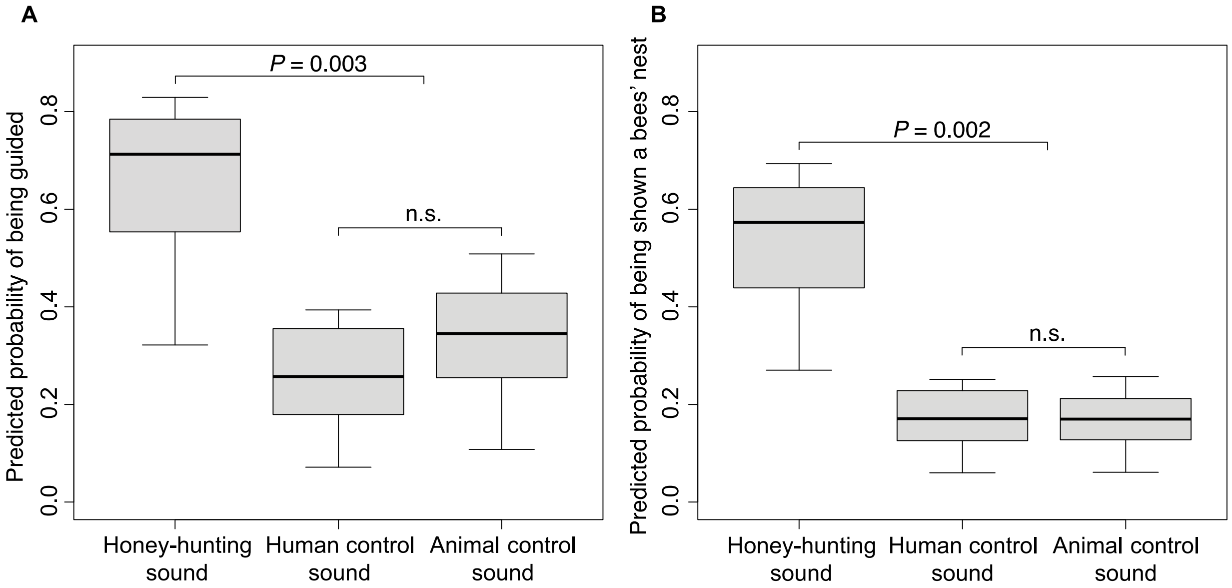
A
B
P = 0.003
n.s.
P = 0.002
n.s.
Predicted probability of being guided
Predicted probability of being shown a bees' nest
0.0
0.2
0.4
0.6
0.8
Honey-hunting sound
Human control sound
Animal control sound

Fig. 2.