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ORIGINAL RESEARCH

Do honey badgers and greater honeyguide birds cooperate to access bees' nests? Ecological evidence and honey-hunter accounts

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Abstract

In parts of Africa, greater honeyguides (*Indicator indicator*) lead people to bees' nests, after which people harvest the honey, and make beeswax and larvae accessible to the honeyguide. In scientific and popular literature, a similar cooperative relationship is frequently described between honeyguides and honey badgers (*Mellivora capensis*), yet the evidence that this occurs is unclear. Such a partnership may have implications for the origins of our own species' cooperation with honeyguides and for the ecology and conservation of both honey badgers and honeyguides. Here, we review the evidence that honey badgers and honeyguides cooperate to access bees' nests, drawing from the published literature, from our own observations whilst studying both species, and by conducting 394 interviews with honey-hunters in 11 communities across nine African countries. We find that the scientific evidence relies on incomplete and second-hand accounts and does not convincingly indicate that the two species cooperate. The majority of honey-hunters we interviewed were similarly doubtful about the interaction, but many interviewees in the Hadzabe, Maasai, and mixed culture communities in Tanzania reported having seen honey badgers and honeyguides interact, and think that they do cooperate. This complementary approach suggests that the most likely scenario is that the interaction does occur but is highly localized or extremely difficult to observe, or both. With substantial uncertainty remaining, we outline empirical studies that would clarify whether and where honeyguides and honey badgers cooperate, and emphasize the value of integrating scientific and cultural knowledge in ecology.

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Introduction

Greater honeyguides (*Indicator indicator*; hereafter 'honeyguides') are known to lead humans (*Homo sapiens*) to bees' nests (dos Santos, 1609; Isack, 1987; Isack & Reyer, 1989; Spottiswoode et al., 2016; van der Wal, Gedi, & Spottiswoode, 2022; Wood et al., 2014), and it has repeatedly been stated that honeyguides similarly guide honey badgers (*Mellivora capensis*, also known as 'ratels'; hereafter 'badgers'; Fincham et al., 2017; Friedmann, 1955, 1958; Sparrman, 1777). Narratives of honeyguides leading badgers to bees' nests can be found in scientific publications, popular science books, and films (Attenborough, 1998; Friedmann & Weber, 1954; May, 1989; Uys, 1974). Despite this widespread belief, it has been argued that cooperation between badgers and honeyguides is fictitious and merely a romanticized or mythologized story of two charismatic animals interacting in an appealingly positive way (Dean, 1985; Dean et al., 1990; Dean & Macdonald, 1981; Short & Horne, 2001). For example, a popular comic nature film titled 'Animals Are Beautiful People' (Uys, 1974) purporting to show footage of badger-honeyguide cooperation was in fact entirely staged using a tame badger trained to follow a taxidermic model of a bird on a fishing line (original production staff member pers. comms. to A.K., Fig. S1). The authenticity of this interspecies cooperative partnership therefore remains unclear.

Written accounts of badger-honeyguide cooperation begin with the honeyguide calling to the badger and conspicuously flying in the direction of a bees' nest, much as honeyguides do when cooperating with humans (Isack & Reyer, 1989). The badger reportedly follows the bird, locates the bees' nest and breaks it open to feed on the honey, beeswax and larvae (Friedmann, 1955). The honeyguide can then supplement its insectivorous diet by feeding on the beeswax, to which it would have very limited access without assistance from other species (Isack & Reyer, 1989). Since both parties are said to benefit from the hypothesized interaction, it would be classed as a 'mutualism' (Bronstein, 2015).

Confirmation of cooperation between badgers and honeyguides could have three broad implications. First, it may shed light on the origin of our own species' cooperation with honeyguides, as it has been speculated that badgers were honeyguides' original partners, before humans replaced or joined them (Friedmann, 1958). Second, if badger-honeyguide cooperation occurs, it is likely rare or declining, potentially due to habitat degradation affecting honeyguides, badgers, and bees, and persecution by humans reducing daytime activity of badgers. Its conservation would require strategies to protect the environment that supports it, both species' willingness to participate and, if it is transmitted culturally, the necessary compatible interspecies knowledge (van der Wal, Spottiswoode, et al., 2022). Finally, badger-honeyguide cooperation would provide a rare example of 'interspecies cooperation' that requires coordinated action from both parties towards a shared goal (Cram et al., 2022). Clarifying its ecology and evolution would offer opportunities for comparative studies with similar examples of signal-coordinated interspecies cooperation (Bayley & Rose, 2020; Caves et al., 2018; Cram et al., 2022; Spottiswoode et al., 2016; Vail et al., 2013; Worsley & O'Hara, 2019).

Here, we collect new data and review existing evidence that badgers and honeyguides cooperate to locate and access bees' nests. First, we interview honey-hunters from 11 communities across Africa, surveying individual and cultural knowledge about the interaction in a standardized way. People in the communities we survey have, for generations, regularly searched for wild honey in habitats with both badgers and honeyguides and are therefore well-positioned to have witnessed potential badger-honeyguide cooperation. Second, we identify the six key steps necessary for the cooperation to take place and review the evidence and feasibility of each step, drawing from published literature, from honey-hunters' observations and from our own studies of badgers and honeyguides. Finally, we integrate these findings and evaluate the support for three possible hypotheses: *Hypothesis 1*: badger-honeyguide cooperation is widespread across Africa; *Hypothesis 2*: badger-honeyguide cooperation does not occur, either because it simply never did or because it has now ceased; and *Hypothesis 3*: badger-honeyguide cooperation occurs but is highly localized and/or difficult to observe.

Part 1: First-hand accounts and beliefs in badger-honeyguide cooperation from a pan-African honey-hunter survey

We interviewed 400 honey-hunters (in March–December 2022) from 11 communities in nine different countries where honey-hunting takes place and where we *a priori* expected honeyguides and badgers to both occur (sample sizes in Fig. 1 and Table S1): Cameroon (mixed culture community: Mboum, Gbaya, Fulani), Eswatini (Swati), Ghana (mixed culture community: Kassena, Sissala, Mosi, Fulani, Nankana), Kenya (Awer), Namibia (Ju/'Hoansi; subset of San), Nigeria (mixed culture community: Afizere, Mambila, Fulani), Malawi (mixed culture community: Chewa, Ngoni, Ngonde, Tumbuka), Mozambique (Yao), Tanzania (north: Hadzabe and Maasai, south: mixed culture community: Hehe, Gogo, Konongo, Kimbu, Nyamwezi, Nyiha, Sangu, Sukuma). Only eight (2%) of interviewees were women, supporting previous studies suggesting that most honey-hunters are men (van der Wal, Gedi, et al., 2022; Wood et al., 2014). We asked (in the mother tongue or *lingua franca*): (1) whether they thought honeyguides

and badgers cooperate and (2) whether they had seen honeyguides interact with badgers, and if so, to describe the interaction. We asked whether they had seen the species 'interact' rather than 'cooperate' to invite the broadest possible observations. We made a *post hoc* distinction between people that described seeing the two species together only at a bees' nest (which might reflect the two species foraging on the same resource without cooperation) and those that said they had (also) seen them interact away from a bees' nests (which typically involved reports of the badger following the calling honeyguide in a manner consistent with putative cooperation). We asked interviewees whether they had seen greater honeyguides and badgers (after asking them to identify photographs of both species) and whether they had honey-hunted with honeyguides. The 11 communities include varying degrees of reliance on cooperating with honeyguides whilst honey-hunting (Table S1), ranging from those who very rarely do so (e.g. in Ghana), to those who almost always seek the help of honeyguides when searching for honey (e.g. Hadzabe in Tanzania, Yao in Mozambique). The inclusion of communities who very rarely cooperate with honeyguides could shed light on the suggestion that humans replaced badgers as the honeyguides' partner species, such that badgers only cooperate with honeyguides where humans do not (Friedmann, 1958). We excluded six interviews in one village in Ghana because none of them had seen a badger, and we could therefore not be sure that they occur there. Therefore, the total number of interviews analysed was 394. A summary of the interview responses per community is presented in Tables S1 and S2.

The interviewees provided their informed consent to participate in this study. Data collection was approved by the Science Faculty Human Ethics Committee at the University of Cape Town (approval no. FSREC 46–2019) and the Institutional review board at the University of California, Los Angeles (study 19–000150). Anonymized answers as given by the honey-hunters interviewed in the study are available via OSF: https://osf.io/2xcrs. All names and precise locations have been removed to preserve confidentiality.

In total, 76 interviewees (19%) said they had seen badgers and honeyguides interact, of which 14 mentioned that they had seen the two species together only at a bees' nest, and 62 described seeing them interact away from a bees' nest. One hundred and eleven interviewees (28%) said they believed badger-honeyguide cooperation occurs. Reports of first-hand observations of badger-honeyguide interaction and belief in cooperation were highest in the three communities surveyed in Tanzania (Hadzabe, Maasai and the community of mixed culture in the south), which together accounted for 71% and 68% of interviewees who had seen the interaction and believed in cooperation, respectively.

In all communities except those in Tanzania, few honey-hunters (mean: 6% per community, range: 0–13%) reported first-hand observations of badger-honeyguide interaction (1 Cameroonian, 2 Nigerian, 10 Malawian, 7 Emaswati, and 2 Yao interviewees; Fig. 1b). Thirty-six interviewees (13% of 274 from these eight communities combined) thought badger-honeyguide cooperation occurs (2 Ju/'Hoansi, 3 Nigerian, 22 Malawian, and 9 Emaswati interviewees). On average, 70% of interviewees outside of Tanzania had seen a badger before (range: 33–100% per community).

In contrast, many interviewees from Tanzania reported that they had seen badgers and honeyguides interacting [Hadzabe: 25 of 41 (61%); Maasai: 8 of 16 (50%); southern Tanzania: 21 of 63 (33%)] and believed that badgers and honeyguides cooperate [Hadzabe: 38 of 41 (93%); Maasai: 7 out of 16 (44%); southern Tanzania: 30 of 63 (48%); Fig. 1b]. All Maasai (n = 16), 36 of 41 (88%) of Hadzabe interviewees and 40 out of 63 (63%) of the southern Tanzanian interviewees reported having personally seen a badger. The exceptionally high rates of belief in, and personal observation of, badger-honeyguide cooperation by Hadzabe honey-hunters persisted even when disregarding five interviewees' accounts (four of whom said they had seen badger-honeyguide interaction) that were questionable or inconsistent as evaluated by M.A., who was well-placed to score responses in this fashion because of her deep familiarity with the local ecology and the interviewees themselves (see Table S2). Similar additional scrutiny of responses was not possible for other communities.

Interestingly, one of the interviewees from southern Tanzania mentioned that the basis for his belief in the two species cooperating was a movie about badger-honeyguide cooperation screened in a local cinema [likely to have been the comic nature film 'Animals Are Beautiful People' by Uys (1974)]. This could have affected the beliefs of others in this community. In the other Tanzanian honey-hunting communities we interviewed (the Hadzabe and Maasai), M.A. and E.A.L. (who are members of these communities) judged it highly unlikely that people were exposed to any movie featuring honeyguides or badgers.

Part 2: Evidence for each step of the interaction from the published literature, honey-hunter surveys, and our own studies of badgers and honeyguides

To review the feasibility of badger-honeyguide cooperation, we break it down into six steps (Fig. 2). For each step, we summarize the relevant evidence, drawing from the published literature, our observations whilst studying both species in Niassa Special Reserve (hereafter 'Niassa') in northern Mozambique where honey-hunting with honeyguides is common (Spottiswoode et al., 2016), our observations whilst studying Hadzabe honey-hunting culture in northern Tanzania, and responses from interviewees. This approach aims to clarify the evidence for the cooperation, by identifying any steps that lack support, which could also help focus future studies.

1. The honeyguide must see a badger

Badgers' and honeyguides' ranges overlap in approximately half of the African continent (BirdLife International, 2022; Skinner & Chimimba, 2005; Fig. 3). Badgers are primarily nocturnal, as noted by 23 honey-hunters we interviewed (1 Cameroonian, 3 Maasai, 12 Malawian, 1 Liswati and 6 southern Tanzanian interviewees). However, our three-year study of badgers at our field site in Niassa revealed that they also forage after sunrise ((C.M.B. & K.S.B. unpubl. data), which is

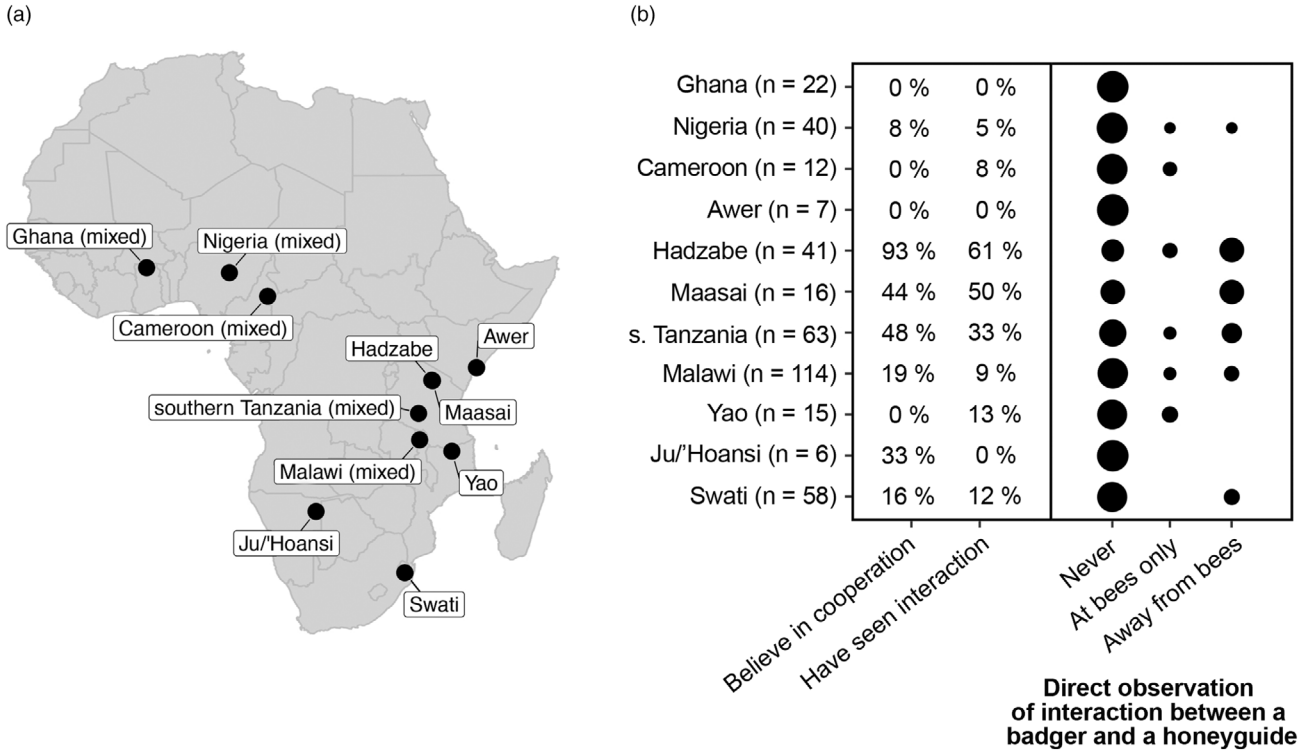

Figure 1 (a) Locations of 11 communities in which we interviewed honey-hunters. (b) A plot indicating, per community: the percentage (%) of interviewees that believed in badger-honeyguide cooperation; the percentage (%) of interviewees that reported having seen badgers and honeyguides interact; a balloon plot indicating the relative frequency of interviewees that had never seen the species interacting, that had only seen them interacting at a bees' nest, or had (also) seen them interacting away from a bees' nest. Balloon sizes indicate the proportion of interviewees from each group that provided each response. Sample sizes are given next to each community name.

supported by research elsewhere (Allen et al., 2018; Begg et al., 2016; Gil-Sánchez et al., 2020; Skinner & Chimimba, 2005; Wood et al., 2021) and is more common where badgers are not persecuted by humans (Begg & Begg, 2002). Therefore, badgers could encounter diurnal honeyguides during the period that they are most active in guiding humans and eating beeswax (early morning and evening, Lloyd-Jones et al., 2022; Spottiswoode et al., 2016). Badgers also occur in places where honeyguides commonly guide humans, meaning that where badgers and honeyguides are sympatric, honeyguides know how to guide and could feasibly cooperate with badgers as they do with humans (Fig. 3d).

2. The honeyguide must display to the badger and fly in the direction of a bees' nest

We have studied honeyguides and honey-hunting cultures in Niassa [Mozambique] since 2013 (C.M.B., K.S.B., C.N.S., D.J.L.-J., D.L.C. and J.E.M.vd.W.) and near Lake Eyasi [Tanzania] since 2004 (B.M.W., J.A.H., M.A.) and have been guided hundreds of times by honeyguides, yet we have never observed one calling to or interacting with a badger, despite both species being common at both locations. Equally, we have studied badger ecology at Niassa since 2003 and have never seen them following or interacting with honeyguides (C.M.B. and K.S.B.).

By contrast, there are second-hand reports of honeyguides giving guiding calls to badgers across most of the honeyguide's range [southern Africa (South Africa, Zimbabwe), East Africa (Kenya, Tanzania) and Central Africa (Democratic Republic of Congo and former French Equatorial Africa); Friedmann, 1955, 1958; Kingdon, 1977]. These sources also report stories of honeyguides giving guiding calls to baboons and other monkeys and to species of mongoose, genet, antelope and lions. We found no recent observations of honeyguides calling to these species, and six principal investigators running long-term studies of wild baboons had never seen baboons and honeyguides interacting (Wood et al., 2014).

In our interviews, 20 interviewees explicitly mentioned witnessing the honeyguide giving its guiding call to a badger whilst away from a bees' nest. Similarly, Fincham et al. (2017) described three occasions of juvenile and adult honeyguides giving guiding calls to a hand-reared young badger. Critically, there was a human observer present in all these cases, so it is impossible to rule out that the honeyguide's call was instead directed at the human, even if the bird appeared to be ignoring them. To remove the confounding effects of human presence, H.A.I. attempted to test the response of a honeyguide to a taxidermic model of an adult

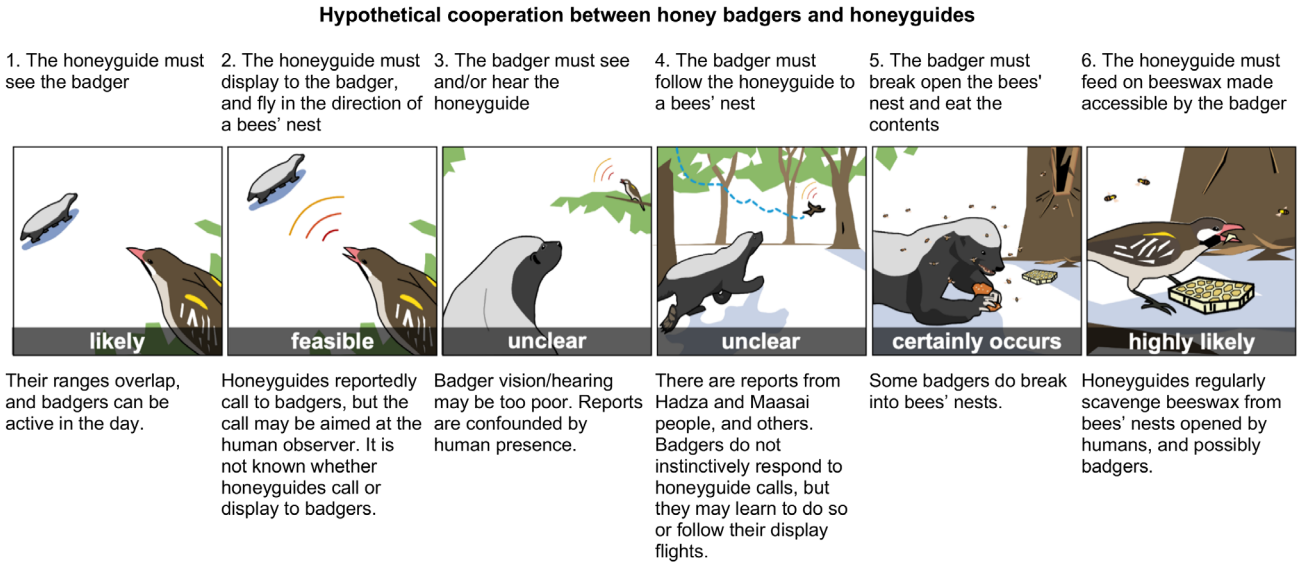

Figure 2 The six key steps of the hypothetical badger-honeyguide cooperation. Beneath each step, we summarize the likelihood that a given step ever occurs in the wild based on available evidence and feasibility. For citations and interview responses that support these summaries, see the corresponding sections 1–6 of the main text. Illustration by Emma Wood.

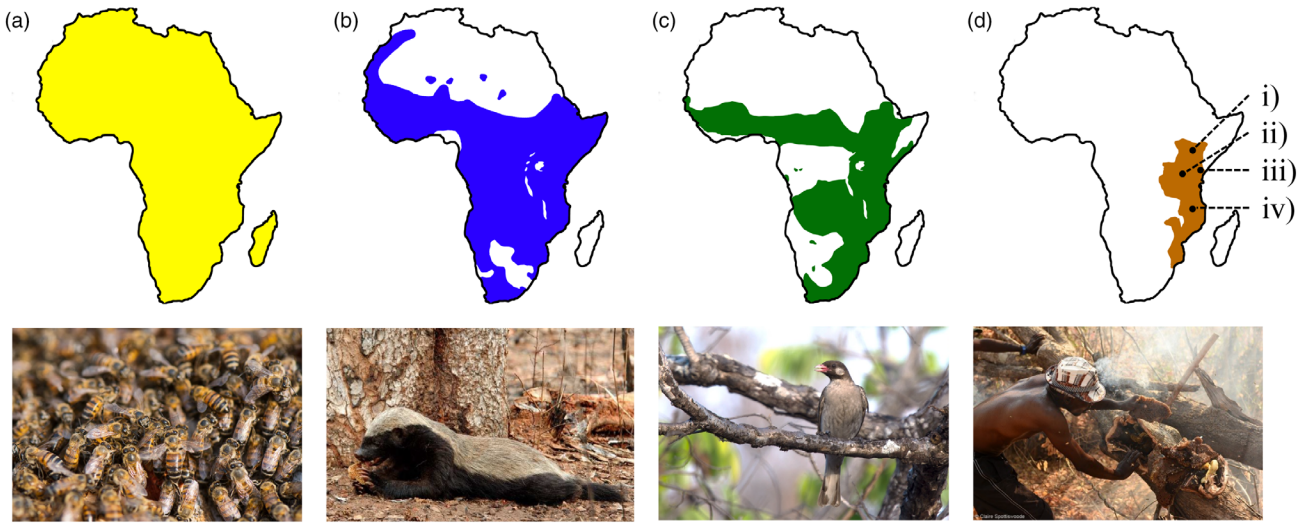

Figure 3 Maps of the African ranges of (a) Honeybees (*Apis mellifera*; Requier et al., 2019), (b) honey badgers (*Mellivora capensis*; Skinner & Smithers, 1990), (c) greater honeyguides (*Indicator indicator*; BirdLife International, 2022), and (d) locations of cultural groups in which honey-hunting with greater honeyguides has been the subject of scientific research. Guiding behaviour is commonplace in these areas and could extend to badgers as well as humans. (i) Boran community in Kenya (Isack & Reyer, 1989); (ii) Hadzabe, Maasai, "Ndorobo" and Sonjo communities in Tanzania (Laltaika, 2021; Wood et al., 2014), (iii) Awer community in Kenya (van der Wal, Gedi, et al., 2022) and (iv) Yao community in Mozambique (Spottiswoode et al., 2016). Photo credits: honeybees and honeyguide: D.L.C.; honey badger: C.M.B.; honey-hunter: C.N.S.

badger mounted on a remote-controlled toy car (Kenya, 1985, Fig. S2). The bird gave a guiding call to H.A.I. (despite his concealment in a small tent) and ignored the taxidermic badger.

A further possibility is that the honeyguide's 'chattering' guiding call is directed at badgers in a context besides cooperation. The guiding call has similarities with, and likely develops from, the begging calls given by nestling honeyguides when begging for food from the host species that raise them (Short & Horne, 2001; Skead, 1951; Cameron J. Blair, D.J.L.-J., C.N.S. & J.E.M.vd.W. unpubl. data). It is therefore plausible that honeyguides may give this call when they encounter an animal they associate with increased availability of beeswax or other sources of food, regardless of whether badgers cooperate in response.

3. The badger must see and/or hear the honeyguide

Human-honeyguide cooperation relies on the honey-hunter seeing and hearing the bird when it approaches the human, typically at a distance of 15–40 m (Fincham et al., 2017; Isack, 1987; pers. obs.). Badgers' foraging ecology depends primarily on their sense of smell (Dean, 1985; Skinner & Chimimba, 2005). One Awer and one Malawian interviewee mentioned that badgers use their sense of smell to detect the direction of a bees' nest, and one Liswati interviewee said they can smell how deep a bees' nest is underground. Badgers are thought to have relatively poor hearing, and their tiny external ears lack pinnae that determine sound directionality (Skinner & Chimimba, 2005; Vanderhaar & Ten Hwang, 2003). Their eyes are small and may favour near-field rather than long-range vision (e.g. Black, 1988; Mendelssohn & Yom-Tov, 1987). Indeed, the apparently poor hearing and vision of badgers makes it possible for researchers to stalk them on foot and capture them using hand nets with relative ease (C.M.B. & K.S.B. pers. obs.). Therefore, badgers could struggle to detect the guiding bird with their limited hearing and visual acuity. Three Hadzabe interviewees mentioned badgers occasionally standing on their hind legs whilst following the honeyguide, perhaps searching for it. It is unknown whether honeyguides alter their guiding behaviour to compensate for sensory differences between badgers and humans (e.g. by approaching badgers more closely). Two Maasai interviewees mentioned honeyguides flying around badgers' heads, though the birds may be investigating or mobbing a potential predator, rather than guiding (Hockey et al., 2005). Two Ghanian interviewees mentioned that they thought badgers eat honeyguides.

4. The badger must follow the honeyguide to a bees' nest

There are three sources of information relevant to the question of whether badgers recognize and follow calling honeyguides. First, there are eyewitness accounts of this behaviour: There are eight observations from various sources reported by Friedmann (1955) and several observations by Tanzanian beekeepers reported by Kingdon (1977). Some of these second-hand accounts describe the badger audibly grunting to the honeyguide, and in some areas, the call people give to attract a honeyguide has been suggested to be an imitation of badger grunts (Estes, 1992; Friedmann, 1955; Kingdon, 1977). To our knowledge, there are no recent or first-hand accounts in the published literature of badgers following calling honeyguides, or any photographic or video evidence. In our interviews with honey-hunting communities, 62 interviewees (21 Hadzabe, 8 Maasai, 7 Malawian, 1 Nigerian, 7 Emaswati and 18 southern Tanzanian interviewees) said that they had observed badgers and honeyguides interacting away from a bees' nest, of which 36 interviewees described the badger calling to the bird (13 Hadzabe: 'se se se'; 2 Malawians: 'hi hi'; 14 southern Tanzanians: thunder, hiss, roar or yawn; 7 Emaswati: whistle). We have heard similar accounts of a badger grunting as it followed a honeyguide (M. Giyai, pers. comm. to K.S.B.). Three other Emaswati interviewees, who did not see badger-honeyguide interaction, said that badgers whistle or hiss when disturbed by humans or their hunting dogs, echoing evidence that badgers vocalize when stressed or aggressive (Kingdon, 1977).

Second, three hand-reared captive badgers did not respond to experimental playback of honeyguide guiding calls, suggesting that any recognition or response is not innate in badgers (Dean, 1985). However, this experiment cannot exclude the possibility that wild badgers learn to follow honeyguide calls. Badgers have relatively large brains that may allow them to learn to exploit new food sources (Benson-Amram et al., 2016; Sheppey & Bernard, 1984). Badgers learn many foraging skills (including how to access bees' nests) when foraging with their mothers (Begg, 2001a; Begg et al., 2005; Prinsloo, 2016), suggesting that the skills required to cooperate with honeyguides could also be socially learnt (Begg et al., 2022; Kingdon, 1977). Furthermore, this experiment cannot exclude the possibility that badgers might, despite their poor vision, follow honeyguides' visual cues (e.g. fluttering flight) rather than vocalizations.

Third, badger-honeyguide cooperation may be feasible given that badgers are frequently seen foraging in association with other species during the day (several species of goshawk and other birds) and night (jackals and owls; reviewed in Begg et al., 2022; Dean & Macdonald, 1981). However, these interactions typically involve other species following a badger to scavenge with no response from, or benefit to, the badger, and they are not thought to be mutualistic (Begg et al., 2022).

5. The badger must break into the bees' nest and eat honey

Badgers are accomplished raiders of human-made beehives and have been observed breaking into wild bees' nests to eat honey (Friedmann, 1958; Johnson, 2018). Fifty-seven interviewees (1 Cameroonian, 21 Hadzabe, 2 Nigerian, 6 Maasai, 6 Malawian, 15 southern Tanzanian, 4 Emaswati and 2 Yao interviewees) who reported having seen badgers and honeyguides interact, specifically described seeing badgers present or feeding at a bees' nest. Of these, four Hadzabe interviewees described the badger breaking the nest open (in three of these cases, the badger removed a stone from the entrance that a human had placed after harvesting). Nine interviewees (2 Hadzabe, 3 Malawian and 4 Emaswati interviewees) mentioned having seen badgers opening bees' nests in the ground or in mounds. Badgers have strong claws and thick skin offering some protection from bee stings (Kingdon, 1977), and they can climb trees to reach wild and hived bees' nests and bird nests (Friedmann, 1958; Marlow, 1983; one Malawian and two Hadzabe interviewees). It is unknown which bee species honeyguides may lead badgers to, but when humans and honeyguides cooperate, the honeyguide primarily guides to African honeybees (*Apis mellifera scutellata* and *A. m. capensis)* and at some locations meliponine stingless bees (Spottiswoode et al., 2016; A.O.K., B.M.W. E.A.L. & G.M.M. unpubl. data). Hadzabe people have pointed out to B.M.W. several *A. mellifera* nests that were recently raided by badgers. On three occasions, Yao honey-hunters, accompanied by D.J.L.-J, have been guided by honeyguides to *A. mellifera* colonies recently attacked by honey badgers. Five Emaswati

interviewees mentioned finding bees' nests previously targeted by badgers, including stingless bees' nests, based on scratch marks they found around the nest entrance.

There are limits to badgers' abilities to access bees' nests: some nests are inaccessible to them (two Hadzabe interviewees had seen badgers unable to break open small bees' nest openings), and they are likely unable to subdue the bees. Several reports, including two Hadzabe interviewees, refer to badgers 'farting' or fumigating bees with their anal scent-glands to subdue them, but this is more likely to be a stress response triggered by stinging bees (Attenborough, 1998; Begg, 2001b; Kingdon, 1989; Lynch, 2000). This pungent smell is also apparent when temporarily capturing badgers to tag them for research purposes (C.M.B. & K.S.B. pers. obs.). One interviewee from southern Tanzania described having seen a badger rolling on the ground and flicking up sand to deter bees.

Whilst badgers often attack beekeepers' hives at night when the bees are docile (Dean, 1985; Johnson, 2018), there are many reports of daylight raids (Begg, 2001b), and one observation details a badger being guided to a bees' nest by a honeyguide during the day, and returning at night to break it open (Kingdon, 1977). In Niassa, we observed a badger feeding on a bees' nest inside a tree trunk it had broken open during the night. At dawn a honeyguide perched silently in the tree above (C.M.B. & K.S.B.; Video S1). We did not observe the honeyguide guiding the badger. This was the only close spatial association that C.M.B. and K.S.B. observed between these species whilst following a young male badger for 35 days over two dry seasons (4 months in 2004 & 7 months in 2005; C.M.B. & K.S.B. unpubl. data).

Badgers are thought to show some degree of individual dietary specialization, for example, being specialists at foraging techniques such as hunting springhares (*Pedetes capensis*) or raiding owl nests (Begg, 2001a; Estes, 1992; Gil-Sánchez et al., 2020). Importantly, this dietary specialization suggests that only a subset of badgers possesses the skills and knowledge to climb trees or access bees' nests (likely learnt from other badgers, usually mothers; Begg et al., 2005) and therefore be a useful partner to a honeyguide.

6. The honeyguide must feed on beeswax made accessible by the badger

Honeyguides frequently scavenge on wax made accessible by a human honey-harvest even if they did not guide a human partner to that bees' nest themselves (Lloyd-Jones et al., 2022), suggesting that they likely do so at nests opened by badgers. Although honeyguides are very likely to have increased access to wax after a badger opens a bees' nest, the scavenging opportunities might vary depending on how much wax the badger consumes (scavenging badgers frequently consume all the wax revealed by human honey-harvests; Lloyd-Jones et al., 2022) and the aggression of the bees (Isack & Reyer, 1989; Short & Horne, 2001). Although we did not directly ask whether interviewees thought honeyguides benefited from the interaction they saw, 15 honey-hunters noted that they had seen honeyguides eating beeswax leftovers after a badger had opened a bees' nest, whilst 13 Emaswati interviewees said badgers deplete the entire bees' nest leaving nothing for honeyguides, and 1 Ju/'Hoansi interviewee noted that honeyguides guide badgers without any reward. Two Emaswati and 4 Yao interviewees mentioned that they believed that honeyguides benefit from badgers, and not vice versa.

Discussion

Our survey of honey-hunter communities indicated that first-hand observations of badger-honeyguide cooperation are rare in eight out of 11 communities (mean: 6% per community) but common in the communities in Tanzania interviewed (Hadzabe: 61%; Maasai: 50%; southern Tanzania community: 33%). Our review of the published scientific literature revealed that although some of the interaction's six key steps are feasible and supported by the literature, key evidence is lacking that honeyguides call or display to badgers and that badgers follow them. Combining our review of the scientific evidence supporting the six key stages of the interaction, our own research and the honey-hunter surveys, we evaluate the support for three hypotheses:

Hypothesis 1: Badger-honeyguide cooperation is widespread across Africa

Overall, the evidence is not consistent with badger-honeyguide cooperation occurring widely across the range of both species. Accounts in the published literature are incomplete or second-hand, and our interview data revealed very few observations of the two species interacting at most locations. Additionally, despite studying badgers and honeyguides for many years, we have never witnessed them interacting. It is therefore highly unlikely that badger-honeyguide cooperation is widespread across Africa, as it appears to be absent even at locations where both species occur and where honeyguides know how to guide humans.

Hypothesis 2: Badger-honeyguide cooperation does not occur, either because it never did, or because it has ceased

For Hypothesis 2 to be true, all those reporting to have seen badger-honeyguide cooperation must be mistaken. Misinterpretations of either species' behaviour are plausible, given that (1) badgers and honeyguides may be seen together at a bees' nest, which could be assumed to be the outcome of cooperation because of honeyguides' well-documented tendency to guide people, (2) honeyguides could follow badgers in anticipation of food becoming available (as a number of other species do; reviewed in Begg et al., 2022; Dean & Macdonald, 1981), potentially even flying ahead to wait at the bees' nest, (3) honeyguides may appear to be calling to a badger, but in fact be calling to the human observer, and (4) badgers could follow a cooperating bird and human (perhaps most plausible in our pre-agricultural ancestors, given most present-day human populations persecute badgers; Begg & Begg, 2002). Belief that the two species cooperate could then rapidly disseminate through oral tradition and persist in local and popular culture. Such cultural embedding may be

particularly likely due to the interaction's uplifting nature, the honeyguides' ability to guide people and the badgers' charisma and boldness, which is celebrated and mythologized in culture (Justice, 2014; Kingdon, 1977). For example, Hadzabe beliefs about badger-honeyguide interactions have arguably acquired a ritualized character (Blench, 2014). Widespread belief in badger-honeyguide cooperation could then promote further misinterpretations when the species are seen near one another. Indeed, a film depicting staged badger-honeyguide cooperation influenced the beliefs of at least one interviewee in southern Tanzania.

Even without the peculiarities of honeyguides and badgers, interview responses can be affected by the passage of time, recall biases and a complex mixture of interviewee–interviewer effects (Bernard et al., 1984). Across all cultures, self-reports of behaviour (or others' behaviour) are subject to inaccuracies, including errors of both omission (leaving out factual details whilst retelling events) and commission (adding details that are not factual). Such inevitable inaccuracies in interview data are one reason why extended periods of fieldwork, preferably conducted by researchers close to the culture at hand, and direct observation of phenomena are a gold standard for empirical social science.

Despite the possibility that misinterpreted observations and mythologized beliefs could reinforce one another, we cannot dismiss our interviewees' observations of badger-honeyguide cooperation. *Hypothesis 2* is therefore incompatible with many reports from the Hadzabe, Maasai and southern Tanzanian communities, and a handful of first-hand accounts in the other groups surveyed.

If badger-honeyguide cooperation has ceased because humans replaced badgers in the partnership with honeyguides (Friedmann, 1958), we would expect badger-honeyguide cooperation to persist (or have recovered) in areas where humans and honeyguides do not cooperate, yet we see no evidence for this.

Hypothesis 3: Badger-honeyguide cooperation occurs but is extremely localized and/or difficult to observe

Our interview data suggest that badger-honeyguide cooperation does occur but is geographically restricted, because relevant observations and beliefs were rare except between Lake Eyasi and Ngorongoro in northern Tanzania and in southern Tanzania (see also Kingdon, 1977). Such geographical restriction is plausible if the skills required to engage in the interaction are socially learnt in both species (Begg et al., 2022; Spottiswoode et al., 2016) and therefore rely on local traditions that may be present in some locations but absent elsewhere (Laland & Hoppitt, 2003). It is also feasible that persecution of badgers has contributed to the geographical restriction of badger-honeyguide cooperation, but further work is needed to confirm or refute this.

The interaction is also likely to be extremely difficult to observe. Years of persecution has resulted in badgers that are fearful of humans (Begg & Begg, 2002), and conspicuous human presence typically disturbs badgers' natural behaviour, as well as causing honeyguides to call to the human rather than the badger. The susceptibility of the interaction to human disturbance may explain why, in our interview data, observations of badger-honeyguide interactions were most common amongst those least likely to disturb it. The Hadzabe (61% of whom reported having seen the two species interact) are hunter-gatherers who are experts at quietly approaching animals to hunt with bows and arrows (including badgers) and whistling to attract honeyguides without alerting other animals (Spottiswoode & Wood, in review; Wood et al., 2014; Wood & Marlowe, 2014). However, such observations were also common in nearby communities that are likely to be much more conspicuous to badgers and honeyguides: the Maasai (who are typically pastoralists) and the southern Tanzanian community (who are typically farmers). Broadly, the available evidence suggests that badger-honeyguide cooperation is difficult to observe because of the confounding effects of human presence.

Suggestions for future studies

We suggest two study designs to test whether and where badgers and honeyguides cooperate. First, to clarify whether honeyguides give guiding calls to badgers without humans present and whether badgers respond by vocalizing and changing course, audio-recording GPS-tracking collars could be fitted to wild badgers in honeyguide habitats. Second, to clarify whether wild badgers respond or move towards honeyguide cues, badgers could be experimentally exposed to remotely triggered playbacks and visual cues (i.e. fluttering honeyguide-like models). Such experiments will be challenging, because wild badgers are difficult to locate, and a large sample size may be required if the behaviour is socially learnt by only a fraction of badgers (see Part 2; Begg, 2001a).

In the interest of improving future research on this topic, we highlight several past errors that have hampered efforts to clarify this issue. First, we urge caution before making strong assertions, because a number of past statements (both in support and in opposition of badger-honeyguide cooperation) have subsequently proven inaccurate. For example, assertions that badger-honeyguide cooperation cannot occur because badgers are exclusively nocturnal, cannot climb trees and do not respond to honeyguide calls, all appear to be over-statements (Dean, 1985; Dean et al., 1990; Marlow, 1983). The title of a recent article indicates 'reciprocal signalling' occurs between badgers and honeyguides, but in fact the observations report honeyguides calling to a badger (or to the humans present) without the badger reacting (Fincham et al., 2017). The clip from a popular 1970s comic nature film staging an interaction between a tame badger and a honeyguide model has been circulated without context on the Internet and falsely interpreted as being from a factual wildlife documentary (Kingston, 2011). Second, it is clear that the experiences and views of peoples who harvest wild honey should have been more thoroughly surveyed by scientists long ago (but see Kingdon, 1977 for a valuable exception). Like all self-reports of behaviour and observations, such data are susceptible to inaccuracies (Sheppey & Bernard, 1984), but they nonetheless provide key insights into the distribution and prevalence of potential badger-honeyguide cooperation.

Conclusion

Overall, our analysis shows that we lack definitive evidence (such as remote audio or video records) of key aspects of potential badger-honeyguide cooperation. In eight of the 11 honey-hunting communities we surveyed, a strong majority of interviewees had never seen the two species interact and did not believe they cooperate. However, first-hand accounts by Hadzabe, Maasai and southern Tanzanian honey-hunters (and a small number from other cultures) are suggestive that badger-honeyguide cooperation may occur at least in parts of Tanzania. Though substantial uncertainty remains, evidence from our complementary approach is therefore consistent with the hypothesis that the interaction does occur but is highly localized or extremely difficult to observe, or both. We hope that further evidence bearing on this relationship emerges and urge those with relevant first-hand observations, oral history accounts and photographs or videos to publish them, but we also urge caution when drawing conclusions.

Notably, in the absence of interview responses from honey-hunting communities, we would have drawn a different conclusion, due to the difficulty of observing natural interactions between badgers and honeyguides, and the resulting lack of direct, recorded evidence that badgers follow honeyguides. This study therefore also highlights the need for scientists to engage more with relevant communities and learn from their views and observations, which have the potential to enrich and accelerate research in diverse fields.

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Conflict of interest

The authors declare that no competing interests exist.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of interview outcomes per community, grouped by country. Main livelihoods are scored with a '+' where the activity is undertaken, and '++' where it is a particularly important activity in this community; note that these are impressionistic scores intended only to give a qualitative overview of each community's livelihoods.

Table S2. Summary, notes on recruitment of interviewees, and summary and highlights of interview responses per community.

Figure S1. A still image from a scene in "Animals Are Beautiful People", a 1974 comic nature film (Uys, 1974). The scene purportedly shows cooperation between a honey badger and a greater honeyguide. However, it was entirely staged using a tame honey badger trained to follow a taxidermic model of a bird, which crew members suspended in front of it using a fishing line.

Figure S2. A picture of the taxidermic model of an adult badger mounted on a remote-controlled toy car with which H.A.I. attempted to test the response of honeyguides. Still image from the BBC nature documentary series "Trials of Life" (1990), specifically from "The Making of The Trials of Life" episode.

Video S1. Clips from a long video recording of a badger feeding on a bees' nest inside a tree trunk it had broken into during the night, and a honeyguide that perched silently in the tree above. The honeyguide did not attempt to guide the honey badger. Recorded by K.S.B. and C.M.B. at Niassa Special Reserve, Mozambique, in 2005.