Understanding the mutualistic interaction between greater honeyguides and four co-existing human cultures in northern Tanzania

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MSc thesis

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Abstract

Greater honeyguides (*Indicator indicator)* eat wax, and to obtain it, they guide people to bees' nests by flying from one tree to another while giving a distinctive chattering call, in the direction of a wild bees' nest. This relationship is mutually beneficial: the hunters harvest valuable honey, and the honeyguides feed on the beeswax leftover from the harvest. In northern Tanzania, multiple human cultural groups live in close proximity in the same geographical area, and most of them practice honey-hunting with the help of honeyguides. Yet, they may differ in cultural traits that determine their relationship with honeyguides. To map this, I visited 12 villages to interview 129 people from the Hadzabe, Ndorobo, Maasai, Sonjo and Datoga cultural groups about their honey-hunting activities and interactions with honeyguides. Specifically, this thesis investigates (i) how important honey and honeyguides are to each human cultural group; (ii) the sounds used by each group to communicate with honeyguides, to test whether honeyguides may have to learn multiple human 'languages' in the same geographical area; (iii) the traditions of each cultural group concerning whether and how to reward the honeyguide after it has shown them a bees' nest; (iv) the methods used by different cultures to subdue the bees, and whether some of these are more sustainable than the use of fire; (v) each cultural group's ownership traditions concerning wild bees' nests, which might incentivise sustainable honey-hunting practices; and finally, (iv) the likely impact of cultural change for the future of the honeyguide-human mutualism. Overall, my results suggest that (i) the human-honeyguide mutualism still thrives in this region, particularly in the Hadzabe and Ndorobo cultural groups who do not practice bee-keeping; (ii) people from each culture are largely consistent in the calls they use to communicate with honeyguides, but that these calls differ between cultures (but are most similar between the Maasai and Ndorobo people who are culturally close despite many differences in lifestyle); (iii) many cultures deliberately 'keep the honeyguide hungry' so it shows them more bees' nests, by either concealing the wax (particularly Hadzabe people) or by pretending not to see the bees' nest the bird shows them (particularly Ndorobo people); (iv) people commonly use methods besides fire to subdue bees, specifically because these methods are less harmful to bees, and particularly a fungus called 'Engishimui' (*Scleroderma verrucosum*); (v) only the Ndorobo currently have ownership traditions associated with wild bees' nests; and (vi) cultural

changes such as bee-keeping were sometimes reported to underlie declines in human-honeyguide mutualism, but that environmental deterioration of bee habitat because of climate change and pastoralist activities seem to be the biggest threats to the still very active Hadzabe and Ndorobo honey-hunting cultures.

Introduction

Since the colonial era, most of the protected areas in Africa have set rules and regulations that restrict human activities in protected areas, and the utilization of wildlife resources is not allowed in many protected areas in Africa and worldwide (Reid, 2001). This is to reduce human environmental degradation and other human impacts that may affect biodiversity (Newmark and Hough, 2000). The Ngorongoro Conservation Area (NCA) in northern Tanzania is notable as a protected area in which humans and wildlife coexist alongside one another, and certain forms of wildlife utilization are permitted (Thompson, 1997). Together with the adjacent Serengeti National Park, the NCA has global importance for biodiversity and was recognized as a UNESCO World Heritage Site in 1979 (Swanson, 2007).

Originally, Ngorongoro and the Serengeti were merged as a single game reserve, and people lived inside both areas (Rogers, 2009). In the 1920s the government of Tanzania wanted to upgrade the Serengeti to a National Park (Nyhus, 2016, Melubo and Lovelock, 2019, Batinoluho, 2019), and so needed to find an alternative area to shift the people who were native to the Serengeti plain, given colonial law that protected and prevented human activities in National Parks (Thompson, 1997). The Serengeti and Ngorongoro were therefore divided into two separate protected areas with different conservation objectives, and the communities who lived in the Serengeti portion was shifted to Ngorongoro to allow the Serengeti to become a National Park (Batinoluho, 2019). In 1959, the NCA was gazetted as a multiple land use area, aiming to develop and protect indigenous peoples' interests, alongside conserving natural resources and promoting tourism activities in the area (Melubo and Lovelock, 2019). An agreement was made when shifting communities from Serengeti to Ngorongoro to allow some communities to utilize certain wildlife resources: the hunter-gatherer communities are permitted through a Memorandum of Understanding with the NCA management to hunt wildlife, whereas hunting is restricted for pastoralist and agriculturalist communities, who are instead permitted to graze their cattle (Kideghesho, 2008, Rogers, 2009, Thompson, 1997).

Thus, after the Serengeti was made a National Park, the colonial-era translocation of human communities has led to a situation where multiple and diverse human cultural groups live in close proximity to one another in the NCA (Thompson, 1997). These can be divided into two main groups with different relationships with the surrounding wildlife: hunter-gatherers (Hadzabe and Ndorobo people) who subsist from hunting of wild animals and gathering of plant resources for their main food, and pastoralists (Maasai, Sonjo and Datoga people) who keep livestock, primary cattle, and rely on palatable grass and water for their livestock (Homewood *et al.*, 1987). Next, I introduce each of these cultural groups in more detail.

Human cultural diversity in the Ngorongoro region

First, the Hadzabe are a small cultural group (population ~ 1200) of hunter-gatherer people who inhabit mainly the Rift Valley floor around Lake Eyasi, as well as the NCA (Wood *et al.*, 2014). They lived in this area before the other pastoralist peoples arrived here, and speak a distinctive click language (Swanson, 2007). Their population is currently in decline and threatened by several factors including pastoralist people (primarily Datoga people) invading their areas, which is problematic because pastoralists' cattle compete with the game animals that the Hadzabe rely on (Marlowe, 2010).

Second, the Ndorobo people (also called Akie people) are also traditionally considered as hunter-gatherers and move around the bush finding their food in a similar way to the Hadzabe (Ashdown, 2002). The term "Ndorobo" is derived from the Maasai word meaning the "poor" or "those with no cattle". The Ndorobo live in a wider area of northern Tanzania, primarily around Kitete Simanjiro, with a smaller population inside the NCA (Shetler, 2007). The Ndorobo have lived alongside the Maasai for many years and have adopted the Maasai language and other Maasai cultural traits, and so their original Akie language is disappearing (Ashdown, 2015).

Third, the Maasai people are considered as pastoralists and have lived nomadically around the Ngorongoro and Serengeti plain since about 200 years ago (Århem, 1985). They belong to the Nilotic language group, and move with their livestock in a constant search for

grazing pasture (Homewood and Rodgers, 2004). The Maasai today dominate the Ngorongoro area, and make up 97% of the resident population (Batinoluho, 2019).

Fourth, Sonjo people are traditionally agropastoral people who grow crops as well as keeping livestock (Adams *et al.*, 1994). The Sonjo are a minority (population ~ 30,000) and currently live west of Lake Natron, north of the NCA, having been pushed away from the Ngorongoro area by the Maasai around 200 years ago (Ojalammi, 2006).

Finally, the Datoga people are pastoralists, although part of the population also practices agriculture (Ndagala, 1991). Only 2% of the Ngorongoro residents are Datoga; they are being driven out by the Maasai by competition for cattle grazing areas, and currently occupy mainly the east and south of the NCA, on the edge of the Rift valley near Lake Eyasi (Borgerhoff-Mulder *et al.*, 1989). In Ol Piro village (amongst other places), the Datoga live beside the Hadzabe (Marlowe, 2002).

Thus, five different human cultural groups live in close proximity in and around the Ngorongoro Conservation Area, and have different relationships with the surrounding wildlife (Nyhus, 2016). Some cultural groups hunt wildlife (Hadzabe, Ndorobo) whereas others instead indirectly compete with wildlife by grazing livestock (Maasai, Sonjo, Datoga). The one wild product that all five cultural groups use is honey. All five cultural groups use honey for different purposes, including food, medicine, and for traditional ceremonies (Tibuhwa, 2012). Honey is obtained from nests of African honeybees (*Apis mellifera scutellata*), but also in smaller quantities from nests of various species of stingless bees (of the bee tribe Meliponini, e.g. genus *Hypotrigona*) (Marlowe *et al.*, 2014). Honey is therefore an important product for these communities (Marlowe, 2010). It is obtained primarily by honey-hunting of wild bees, though some communities, with encouragement from the government and NGOs, also practice bee-keeping (of honeybees) with man-made beehives (Marlowe, 2002). The only cultural group who do not interact directly with bees are the Datoga, who instead obtain honey by trading with other cultural groups.

The human-honeyguide mutualism

In this thesis, I investigate the consequences of this human cultural variation, and shared need to obtain honey, for a unique form of human-wildlife interaction: cooperation with a bird that facilitates human predation on honeybee nests to obtain their honey. This is the mutualism between human honey-hunters and the greater honeyguide (*Indicator indicator*). From the human perspective, this mutualism exists because wild bees are hard for humans to find by themselves. For many centuries, greater honeyguides have been known to guide people to bees' nests. Responding to the honey-hunter's call, a honeyguide flies from one tree to another while giving a distinctive chattering call, leading the hunter to a wild bees' nest. This relationship is mutually beneficial: the hunters harvest valuable honey, and the honeyguides feed on the beeswax leftovers from the harvest (Isack & Reyer, 1989; Spottiswoode, Begg, & Begg, 2016; Wood, Pontzer, Raichlen, & Marlowe, 2014). This close cooperation and communication between humans and wildlife is more commonly observed in trained or human-habituated animals such as in zoos, or in foraging partnerships involving domestication or coercion (e.g., hunting with dogs or falcons), but is very rare in free-living wild animals (Isack, 1999).

The cooperation between honeyguides and humans is an example of a mutualism, which is an interspecific interaction that is mutually beneficial. While the ecology and evolution mutualisms has captivated the research community worldwide and been extensively studied (Bronstein, 1994), mutualisms between humans and wildlife are rare and less studied (Smith *et al.*, 2009, Wood *et al.*, 2014, Spottiswoode *et al.*, 2016, Gruber, 2018). Research on the human-honeyguide mutualism so far has focused particularly on the honeyguide behaviors used to direct honey-hunters to honey, and the diversity of sounds used by honey-hunters to call in the honeyguides (Isack and Reyer, 1989, Spottiswoode *et al.*, 2016). Strikingly, the sounds that local honey-hunters use to call honeyguides have been observed to differ between African countries: the Hadzabe people in northern Tanzania communicate with honeyguide with a whistled melody, while the Yao people in northern Mozambique give a 'brrrr-hm' sound to communicate with the bird (Spottiswoode *et al.*, 2016; Wood *et al.*, 2014). Honeyguides appear to have learnt these cultural differences in the humans they interact with, since they respond preferentially to

humans giving these sounds (Spottiswoode *et al.*, 2016, Spottiswoode & Wood unpublished data).

Aims of this thesis: understanding variation in the human-honeyguide mutualism in the Ngorongoro region

The Ngorongoro Conservation Area is a particularly interesting region to study human-honeyguide mutualism because, as introduced above, it is rich in human cultural diversity. Multiple cultural groups live in close proximity in the same geographical area and have coexisted with wildlife for many years. Each cultural group has its own cultural differences associated with their different lifestyles, from hunting and gathering to livestock keeping, but remarkably most (four out of five) of them practice honey-hunting with the help of honeyguides.

Yet, they may differ in cultural traits that determine their relationship with honeyguides. For example, they may use different sounds to communicate with honeyguides, raising the question of how the birds can cope with multiple different sounds (approximately analogous to languages) used to signal to them. In addition, cultures vary in their systems of rewarding the honeyguide with wax: honey-hunters in some cultures elsewhere in Africa specifically reward the birds with pieces of wax as a signal of gratitude and to motivate the birds to lead them again (Isack and Reyer, 1989). By contrast, it has already been documented that Hadzabe honey-hunters burn or bury the wax to keep the honeyguide hungry, in the expectation that the honey-hunter will be guided to another bees' nest (Wood *et al.*, 2014). We do not yet know how this impacts on the stability of the mutualism, including for other cultural groups in the same area who may have different systems of reward.

Cultures may also differ in traits that have implications for the sustainability of honey-hunting. Some cultures (but not others) have traditions of ownership of wild bees, whereby honey-hunters have ownership of the bees and the tree that houses their bees' nest, and protect them from other honey-hunters (Bradbear, 2009). This should give an incentive for sustainable harvesting of honey, such as not completely destroying the tree or bee colony when harvesting it. Similarly, there is variation in methods used to subdue the bees. Honeybees sting predators to

defend their colony from predators such as honey-hunters (Koffler *et al.*, 2021). Different colonies of bees differ in how aggressive they are: some are extremely defensive and will attack the predator soon after it arrives, whereas other will only sting intruders after they start harvesting (Johnson and Hubbell, 1974). Many honey-hunters use fire to subdue the bees, which dims the bees' awareness and reduces their ability to defend themselves, but has other ecological effects such as causing bees to desert their nests and, in some cases, sparking wildfires that destroy bee habitat (Campbell *et al.*, 2018). Some cultures have devised other methods to subdue bees besides the use of fire, such as using aromatic herbs (Kraft and Venkataraman, 2015), which should reduce these negative ecological effects, and so make honey-hunting more sustainable. It is therefore valuable to understand and document the techniques used by different traditional societies to subdue bees.

Finally, while the relationship between honeyguides and people is likely to have existed for many years (perhaps deep into our evolutionary history; Wrangham, 2012), there is concern that it is likely to change through space and time (Isack, 1998), owing to cultural changes in human communities (such as beekeeping taking the place of honey-hunting), and to environmental changes caused by human activities that may affect bee populations. Thus, my main questions for this thesis are divided into two parts: in part one, I investigate cultural variation in the mutualistic interaction between humans and the honeyguides (questions i-iii), and in part two I investigate the sustainability of the resource between humans and bees (questions iv-vi). I ask:

(i) How important are honey and honeyguides to each human cultural group?

(ii) Do the four cultural groups use the same or different sounds to communicate with honeyguides, such that honeyguides may have to learn multiple human 'languages'?

(iii) What are each cultural group's traditions of rewarding the honeyguide (or not) after it has shown them a bees' nest?

(iv) What methods do different cultures use to subdue honeybees, and are some of these more sustainable than the use of fire?

(v) What are each cultural group's traditions of ownership of wild bees' nests (if any), which might incentivise sustainable honey-hunting practices?

(vi) What is the likely impact of cultural change for the future of the mutualism?

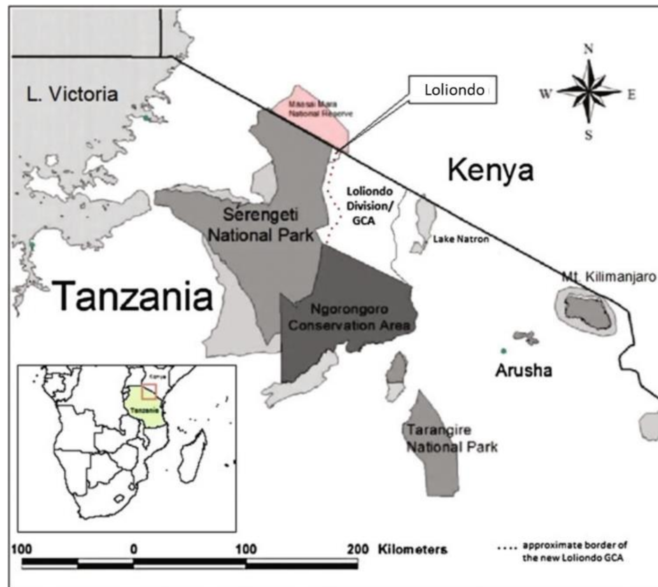
Methods

Study area

I conducted the majority of my data collection in the Ngorongoro Conservation Area (NCA; 8292 km^2), in the northern part of Tanzania in the Ngorongoro District, and centered on latitude 3°10' S and longitude 35°25' E. The NCA is connected to the Serengeti National Park and is part of the Serengeti-Mara ecosystem. It is surrounded by other protected areas including the Maswa Game Reserve, Serengeti National Park, Ikorongo Game Reserve, Loliondo Game Control Area, and Lake Manyara National Park through the Upper Kitete Wildlife Corridor (Batinoluho, 2019). The NCA was established as an alternative location for the displaced communities who were the rightful residents of the Serengeti, when the Serengeti was established as a National Park and the communities accepted to move from the Serengeti to the Ngorongoro highlands (Thompson, 1997). In 1959, it was first established as a multiple land use area according to NCAA Ordinance No. 413 and acts as a wildlife corridor connecting the Ngorongoro and Serengeti ecosystems (Figure 1A).

I also worked at several locations outside the NCA (Figure 1B). First, I interviewed certain Hadzabe communities in the vicinity of Lake Eyasi in the southern part of the Gregory Rift Valley, south-east of the Serengeti Plains and the NCA. Second, I interviewed a Ndorobo community at Makao in the Maswa Game Reserve near the western boundary the NCA, and at Leshule and Olmoti villages located in Kitwai B in Simanjiro District, 250 km to the south-east of the NCA. Finally, I interviewed a Sonjo community in Tinaga village just east to the town of Loliondo, near the Kenyan border (Bartels, 2016) and surrounded by protected areas, including the Masai Mara National Park to the north (in Kenya), the Serengeti National Park to the west, the Ngorongoro Conservation Area to the south, and Loliondo Game Control Area (Gardner, 2012).

A



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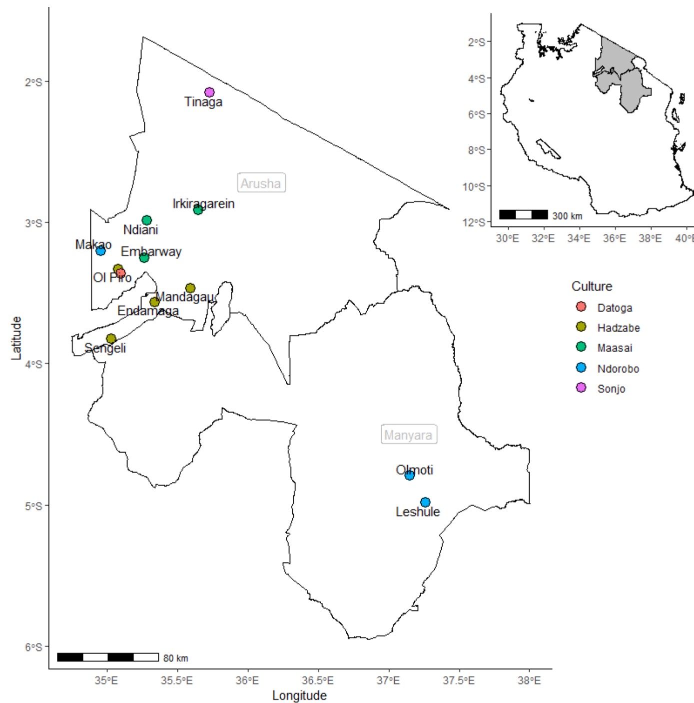

Figure 1: (A) Map of the region showing the relevant protected areas and parks in northern Tanzania where some of the five cultural groups (Hadzabe, Ndorobo, Maasai, Sonjo and Datoga) live. From (Bartels, 2016). (B) The 11 villages where I conducted interviewed, and their associated cultural groups: Hadzabe (Sengeli, Endamaga, Ol Piro, Mandagau), Ndorobo (Olmoti, Leshule and Makao), Maasai (Embarway, Irkiragarein and Ndiani), Sonjo (Tinaga) and Datoga (Ol Piro). Administrative districts are labelled in grey.

Data collection

Data were collected through (i) interviews and (ii) direct observations in the field, whereby I participated in natural honey-hunts with each of the four cultural groups who hunt honey. Fieldwork was carried out from September to December 2020. I interviewed 129 people (all men) in 12 villages, spending approximately 30 minutes interviewing each participant, yielding a total of 65 hours of interviews. The interview questionnaire is provided in Appendix 1. Additionally, I participated in 16 honey-hunting trips and made sound, video and GPS recordings of all activities. This gave me first-hand experience of honey-hunting in each of the four cultures who honey-hunt (i.e. all except the Datoga), and allowed me to qualitatively validate the interview responses, but I did not analyze quantitative data from these trips in this thesis. Sample sizes for each cultural group are summarized in Table 1.

Participants were selected with the help of the local leaders in the village, who assisted by identifying individuals who were known honey-hunters. First, I read these potential participants an informed consent script (provided in English in Appendix 2) in a mutually understood language (Kiswahili or Maa), and asked them to sign with a thumbprint if they were willing to participate. I then made sound recordings (using a Sony M10 digital recorder) of all interviews where participants agreed to be recorded, and took a photograph of all individuals who agreed to be photographed. For those individuals who declined to be recorded but accepted to be interviewed, I wrote down their answers to the questions. I took utmost care to avoid the research participants sharing information, especially the content of the questionnaire and the observations given in reply. To do so, I ensured that participants who were selected to be interviewed were separated from one another or their friends until when the interviews were over. Data collection protocols for this thesis were approved by the University of Cape Town Science Faculty Research Ethics Committee (approval code FSREC 057 – 2020).

Table 1: Cultural groups, number of participants interviewed, number of villages, and the number of honey-hunting trips conducted during data collection from September to December 2020.

Cultural group	Participants	Villages	Honey-hunting trips
Hadzabe	29	4	2
Ndorobo	24	3	4
Maasai	27	3	3
Sonjo	30	1	4
Datoga	19	1	0
Total	129	12	13

Statistical Analysis

I used R 3.5.0 (R Core Team 2018) for all data processing, analyses and visualizations. In the case of categorical answers to interview questions, I summed the count for each category, per cultural group. To test whether proportions of different answers within a cultural group significantly differed between cultures, I performed Fisher's exact tests using the fisher.test function in base R. When $p < 0.05$, I explored which pairs of cultures significantly differed, using the pairwise_ fisher_test function in the 'rstatix' package (Kassambara, 2021), adjusting p-values for multiple comparisons according to the Holm method. When answers were numeric count data (age or time), I tested for differences between cultural groups at the individual level with a generalized linear mixed model (GLM) with a Poisson distribution using the 'lme4 package' (Bates *et al.* 2015), in which the response variable was the individual count of interest, the predictor variable the cultural group, and village the random factor. Assumptions of normality and homoscedasticity for GLMs were assessed by visual inspection of residuals and normal probability plots. To investigate which pairs of cultures significantly differed, I calculated contrasts (Tukey HSD method, $\alpha = 0.05$) between Estimated Marginal Means using the 'emmeans' package (Lenth 2020). When all pairwise comparisons were $p > 0.05$, I report the overall p-values for the model using the Anova function in the 'car' package (Fox and Weisberg 2019), which calculates Type III Wald χ^2 tests. Throughout the thesis, only significant pairwise comparisons ($p < 0.05$) are given in the text and in graphs.

Results

(i) How important are honey and honeyguides to each human cultural group?

(a) What is honey used for, and how important is selling honey for each culture?

All respondents said they use honeybee honey. Besides for food, honeybee honey was used for medicine, alcohol and in ceremonies, to different extents across the cultural groups (Figure 2A). Datoga people use honey only for alcohol and ceremonies, and not as food or medicine. Many respondents in the other cultural groups said they do use honeybee honey as medicine: Hadzabe (34%), Ndorobo (4%), Maasai (33%) and Sonjo (37%). Especially the Maasai (85%) and Datoga (95%) make alcohol from honeybee honey, and the Ndorobo (29%) and Sonjo (63%) do so to a lesser extent. The use of honeybee honey for traditional ceremonies seemed to be especially important for Datoga (100%), Maasai (67%) and Sonjo (73%) respondents, and less so for Ndorobo (25%) respondents. Informal conversations with Hadzabe and Ndorobo honey-hunters made it apparent that honey is the second most important palatable food, after wild meat.

Stingless bee honey was also widely used: 100% of Hadzabe, Ndorobo and Maasai, 97% of Sonjo and 58% of Datoga said they use stingless bee honey. Honey from stingless bees is used for food as well in medicine, and particularly used as food by Hadzabe (97%) and Ndorobo (83%) respondents, compared to Maasai (48%), Sonjo (47%) and Datoga (5%) respondents (Figure 2B). Many Hadzabe (28%), Ndorobo (54%) and Maasai (78%) and Ndorobo (54%) respondents reported that they also use stingless bee honey for medicine.

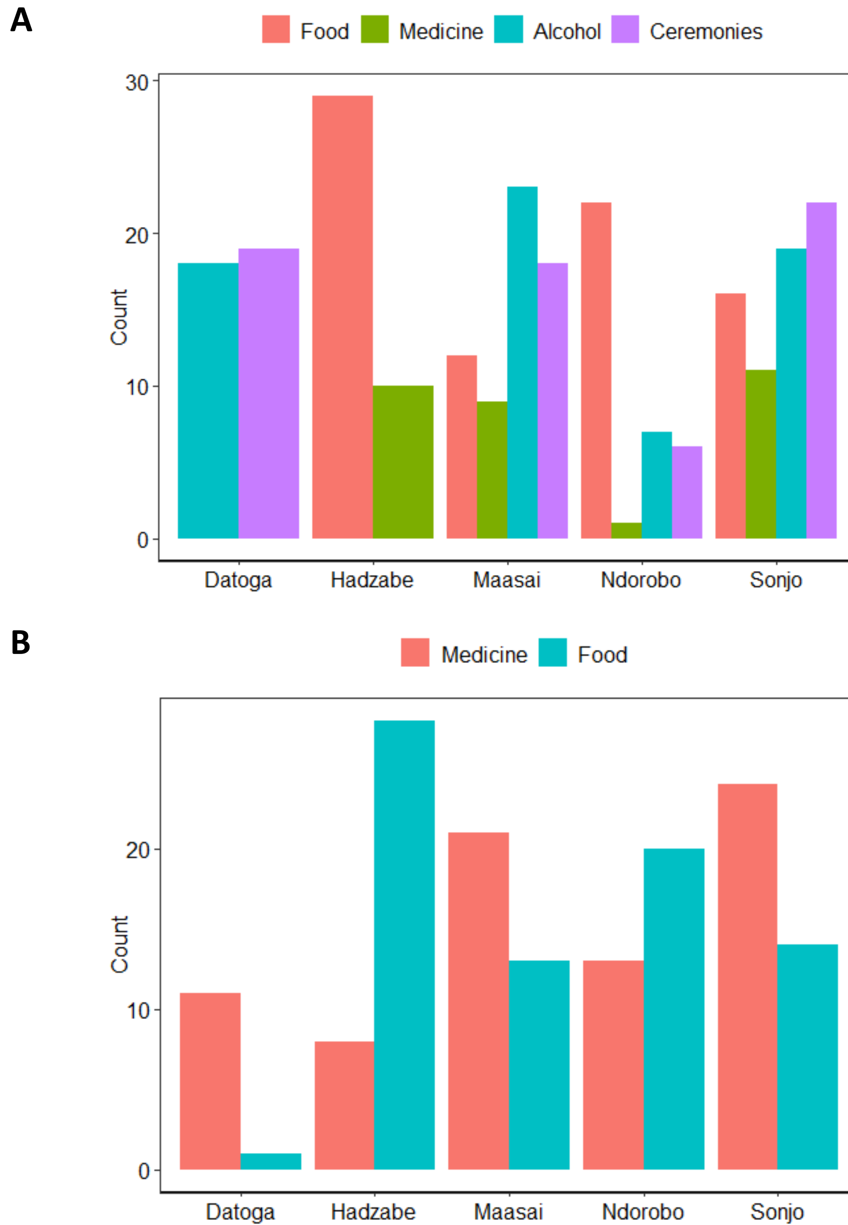

Figure 2: Variation in honey use among cultural groups. Some people gave multiple answers, so the bars do not sum to 100%. (A) Honeybee honey is widely used as food and medicine (except by Datoga people), and to brew alchohol and for traditional ceremonies (excect by Hadzabe people). (B) Stingless bee honey is also used by all five cultural groups as both food and medicine (and never for alcohol or ceremonies).

All but one out of 110 subjects across the four honey-hunting cultural groups responded that selling honey is important. The percentage of subjects that responded that selling honey is “very important” (rather than little or not important) was lower in the Ndorobo (50%) than in the Hadzabe (69%), Sonjo (80%), Maasai (67%), although these percentages were not significantly different (Fisher’s exact test, p = 0.14; Figure 3). The importance of selling honey depends not only on how much honey people can obtain, but also on how easily they are able to sell it. Narrative responses indicated that the Hadzabe, Sonjo, and Maasai have better market access for selling honey, while the Ndorobo people have fewer market opportunities (20% of Ndorobo people commented that they suffer from lack of market access for honey).

Variation in market access was also reflected in the market price for honey, which was lowest for Ndorobo people for both honeybee and stingless bee honey: the price for 20 litres of honeybee honey was given as 100,000–150,000 Tanzania Shillings (TZS) for Maasai, 100,000–110,000 TZS for Sonjo, 70,000–100,000 for Hadzabe and 35,000–50,000 TZS for Ndorobo respondents. Stingless bee honey was much more valuable per litre than honeybee honey: the price for 1 litre of stingless bee honey was given as 20,000–30,000 TZS for Maasai, 5,000–20,000 TZS for Sonjo, 10,000–15,000 for Hadzabe and 7,000–10,000 TZS for Ndorobo respondents.

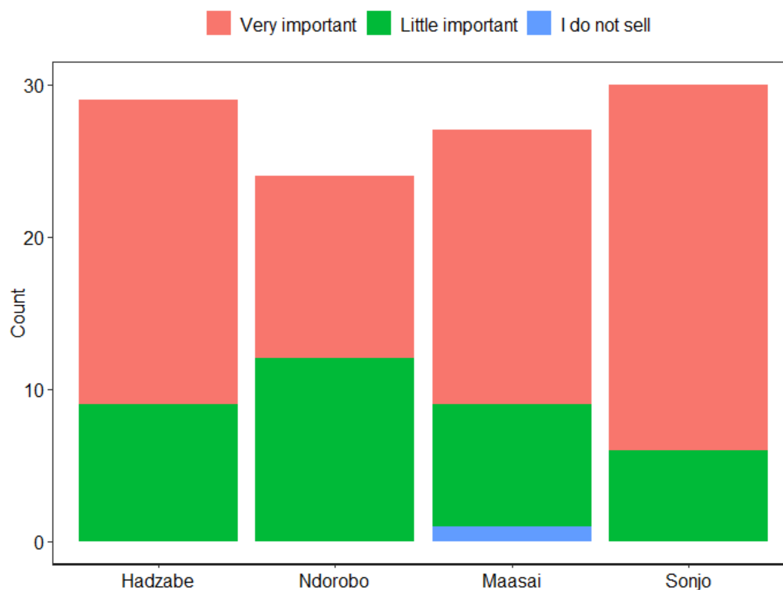

Figure 3: The importance of selling honey was not significantly different between the four honey-hunting cultural groups.

(b) How important is honey-hunting and honeyguides to obtain honeybee honey?

Of the five cultural groups surveyed, the Datoga is the only one that does not honey-hunt: they buy honey from the other cultural groups who are specialised honey-hunters. By contrast, all the Hadzabe and Ndorobo respondents reported that they get all their honey exclusively from honey-hunting. The Maasai and Sonjo respondents reported that they get their honey from honey-hunting (100% and 97% respectively), from beehives (33% and 40% respectively), and from buying from other honey-hunters when they need more honey than they are able to harvest themselves (15% and 17% respectively) (Figure 4).

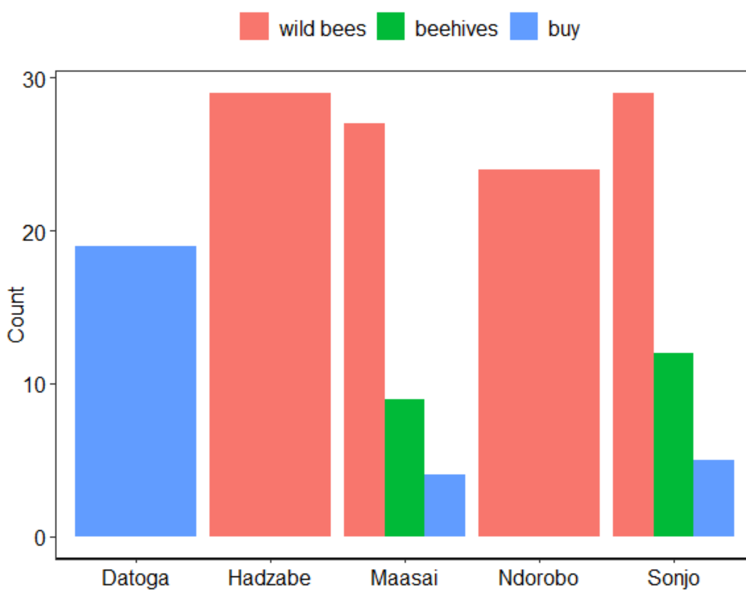

Figure 4: Sources of honey per cultural group: Hadzabe and Ndorobo completely depend on honey-hunting to get honey, while the Maasai and Sonjo get their honey from other various sources. Datoga people do not honey-hunt and only buy honey from other cultural groups. Some people gave multiple answers, so the bars do not sum to 100%.

Among the four cultural groups that honey-hunt, the Hadzabe people seem to be the most specialized and active honey-hunters. To assess which cultural group(s) is/are most specialized and with more active honey-hunters, I asked whether subjects (i) explicitly planned honey-hunting trips for this purpose, or whether they opportunistically looked for honey while they were busy with other activities such as tending livestock (Figure 5A); and (ii) how often they

go honey-hunting per month in the honey-hunting high season (Figure 5B). Subjects from all four cultural groups mentioned that they planned trips for honey-hunting, but the Hadzabe stood out as being the only cultural group where everyone reported that they planned trips specifically for honey-hunting (Figure 5A). By contrast, respondents from the other three honey-hunting cultural groups included several opportunistic honey-hunters (33% of 27 Maasai, 25% of 24 Ndorobo, and 10% of 30 Sonjo; Figure 5A). The proportion of respondents that reported that they planned trips specifically for honey-hunting was significantly different between cultural groups (Fisher's test, $p = 0.001$; Figure 5A): it was higher in the Hadzabe respondents compared to the Ndorobo (Fisher's pairwise test: $p = 0.03$) and Maasai (Fisher's pairwise test: $p = 0.004$) respondents. Moreover, Hadzabe people seem to be the most active honey-hunters because they go honey-hunting significantly more often in the honey-hunting high season compared to all other cultural groups (GLM, Poisson, Ndorobo: $p = 0.001$ Maasai: $p = 0.002$; Sonjo: $p < 0.001$; Figure 5B).

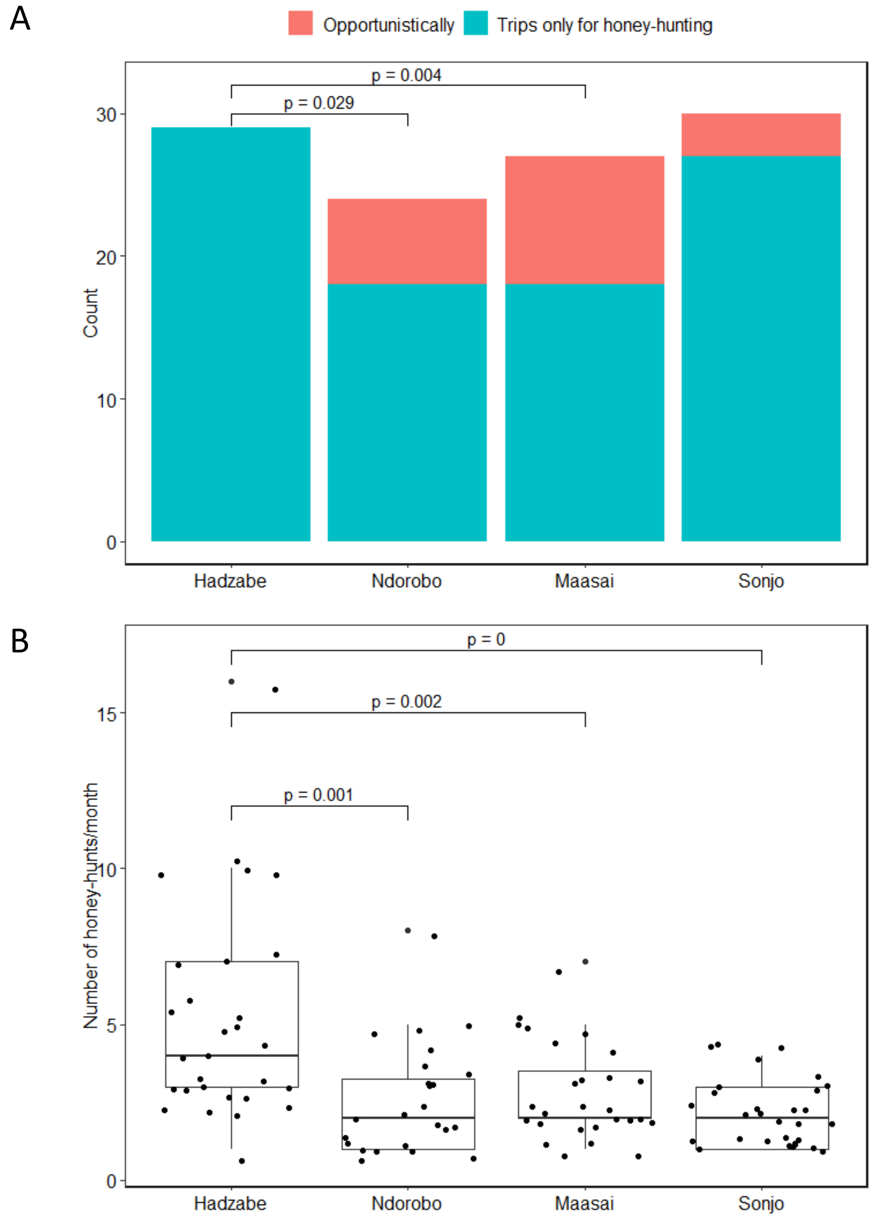

Figure 5: Hadzabe people are the most specialized and active honey-hunters to the other cultural groups, in terms of (A) proportions of trips planned specifically for honey-hunting and (B) frequency of monthly honey-hunting trips in the honey-hunting high season.

Overall, across cultural groups, 99% of subjects (all except one Sonjo person) reported that they are familiar with the bird that guides people to bees' nests (i.e. honeyguides). They reported that the name of this in their language is respectively 'Tikiliko' (Hadzabe), 'Kecheiyante' (Ndorobo), 'Enjoshoroy' (Maasai), and 'Ngishiroy' (Sonjo). Overall, across all groups, 75% of

subjects responded that they “always” or “most of the time” rely on honeyguides to assist them in providing information about the location of bees’ nests (Figure 6). 97% of Hadzabe respondents indicated that they are “always” or “most of the time” reliant on honeyguides, which was significantly different to the other cultural groups (Fisher’s test, p = 0.002): it was higher in Hadzabe respondents (69%) compared to the Ndorobo (63%; pairwise Fisher’s test, p = 0.015), and Sonjo (60%; pairwise Fisher’s test, p = 0.006) respondents.

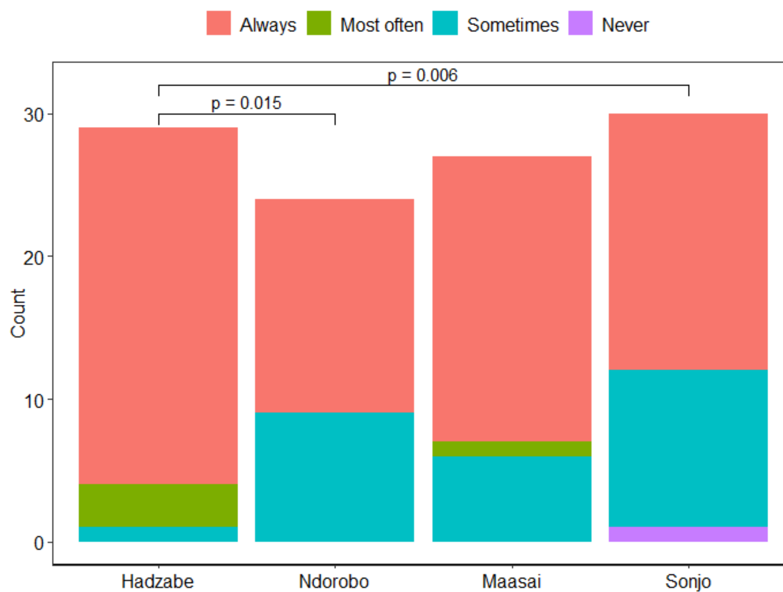

Figure 6: Subjects in all four honey-hunting cultures report that they rely on honeyguides, although to different extents. The proportion of honey-hunters that rely on honeyguide is shown in three categories: always, most often, sometimes or never.

(ii) What calls do honey-hunters use to attract and communicate with honeyguides?

As introduced above, honey-hunters often communicate with honeyguides using specific calls. Therefore I asked subjects to specify what call(s) they used to attract honeyguides (referred to as ‘attracting calls’), as well what call(s) they used to maintain their attention while following honeyguides (referred to as ‘guiding calls’). All respondents who honey-hunt (n = 110) indicated that they do use specific calls to attract honeyguides. Overall, these calls varied across cultures

yet were remarkably consistent within cultures, even in different villages far apart from one another and closer to the villages of other cultures (Figures 7 and 8). These are reported in detail in the next sections. All sounds that were different combinations of words and phrases in the cultural group's own human language are pooled as "words".

(a) *Do cultural groups have different attracting calls?*

Variation in calls reported to be used to attract honeyguides across villages and cultures is shown in Figure 7. Across the four Hadzabe villages, in two villages (Mandagau: n = 3 and Ol Piro: n = 6) respondents reported that they used "words" to attract honeyguides; in Endamaga (n = 10) all but one subject (who used "whistle") reported that they used "words", while in Sengeli (n = 10) everyone reported that they used whistles. All Ndorobo subjects in Olmoti (n = 10), Makao (n = 10) and Leshule (n = 4) reported that they use "Trill-Grunt" to attract honeyguides. Of the Maasai villages, 100% of subjects in Ndiani (n = 10) and 90% of subjects in Irkiragarein reported that they used "Trill-Grunt+Words", while the remaining subject reported that he used "Trill-Words" to attract honeyguides. In the Sonjo village of Tinaga (n = 28), 93% of respondents reported that they use "whistle" as the attracting call, one person used "Whistle-Click", and another person used "Whistle-Grunt".

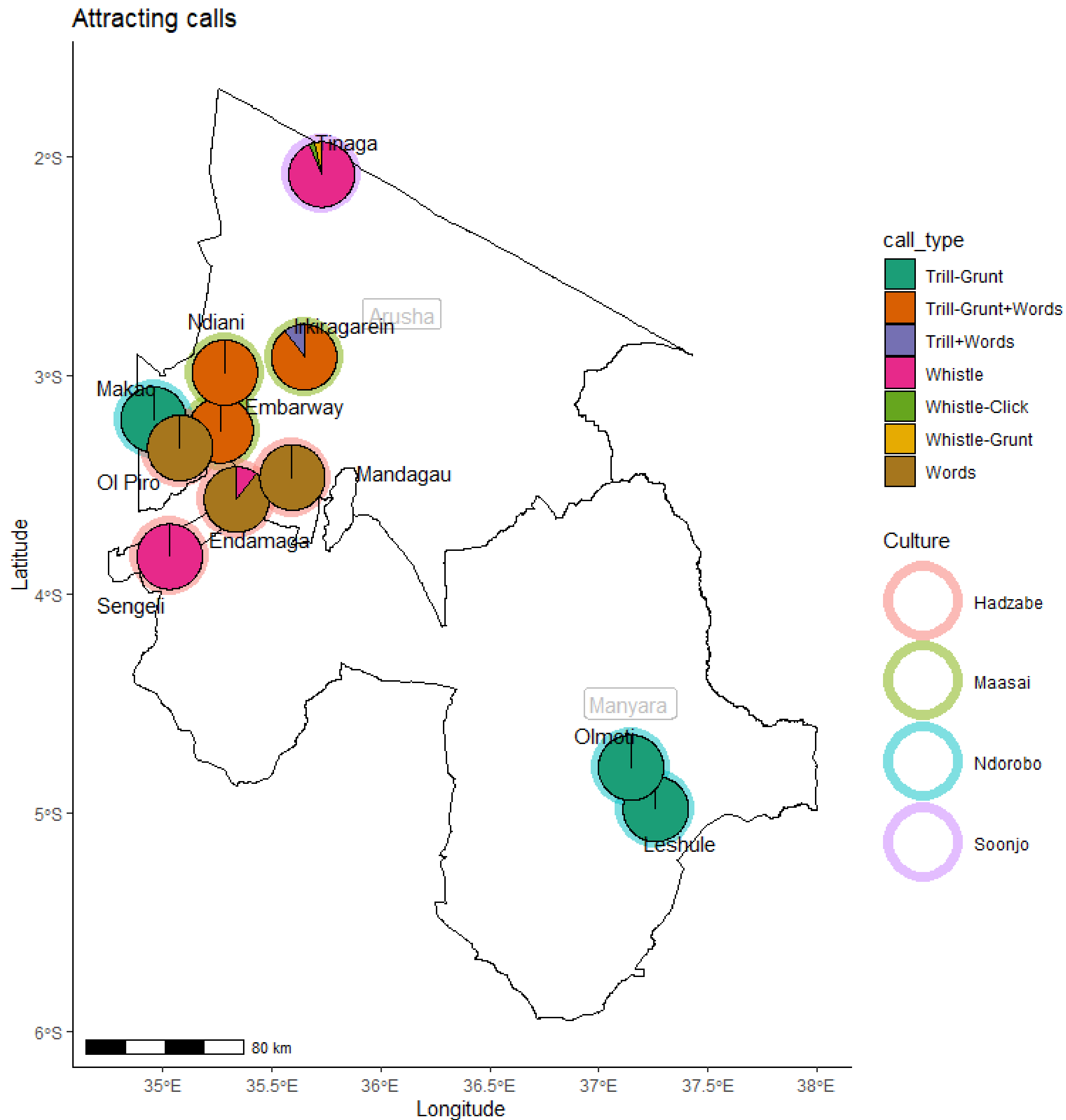

Figure 7: The proportions of different attracting calls that respondents reported they used, per village.

(b) *Do cultural groups have different guiding calls?*

Variation in calls reported to be used while following a guiding honeyguide across villages and cultures is shown in Figure 8. All 29 Hadzabe subjects across four villages (Mandagau: n = 3, Endamaga: n = 10, Sengeli: n = 10, Ol Piro: n = 6) reported that they used “whistle” as the guiding call. In two out of three Ndorobo villages (Olmoti: n = 10 and Leshule: n = 4), all subjects reported

that they used "Trill-Grunt+words", while in the third Village (Makao), 2 of 10 (20%) reported that they use "Words" and 80% reported that they use "Trill-Grunt+words". The Maasai in Embarway (n = 8) and Ndiani (n = 9) all reported that they use "Trill+words", while 9 out of 10 subjects (90%) in Irkiragarein reported that they used "Trill+words". In Tinaga (n = 30), the only Sonjo village surveyed, one respondent reported that he used "Whistle" and another that he used "Whistle-Grunt", and the remaining 28 subjects that they used "Whistle-Click" as the guiding calls (Figure 8).

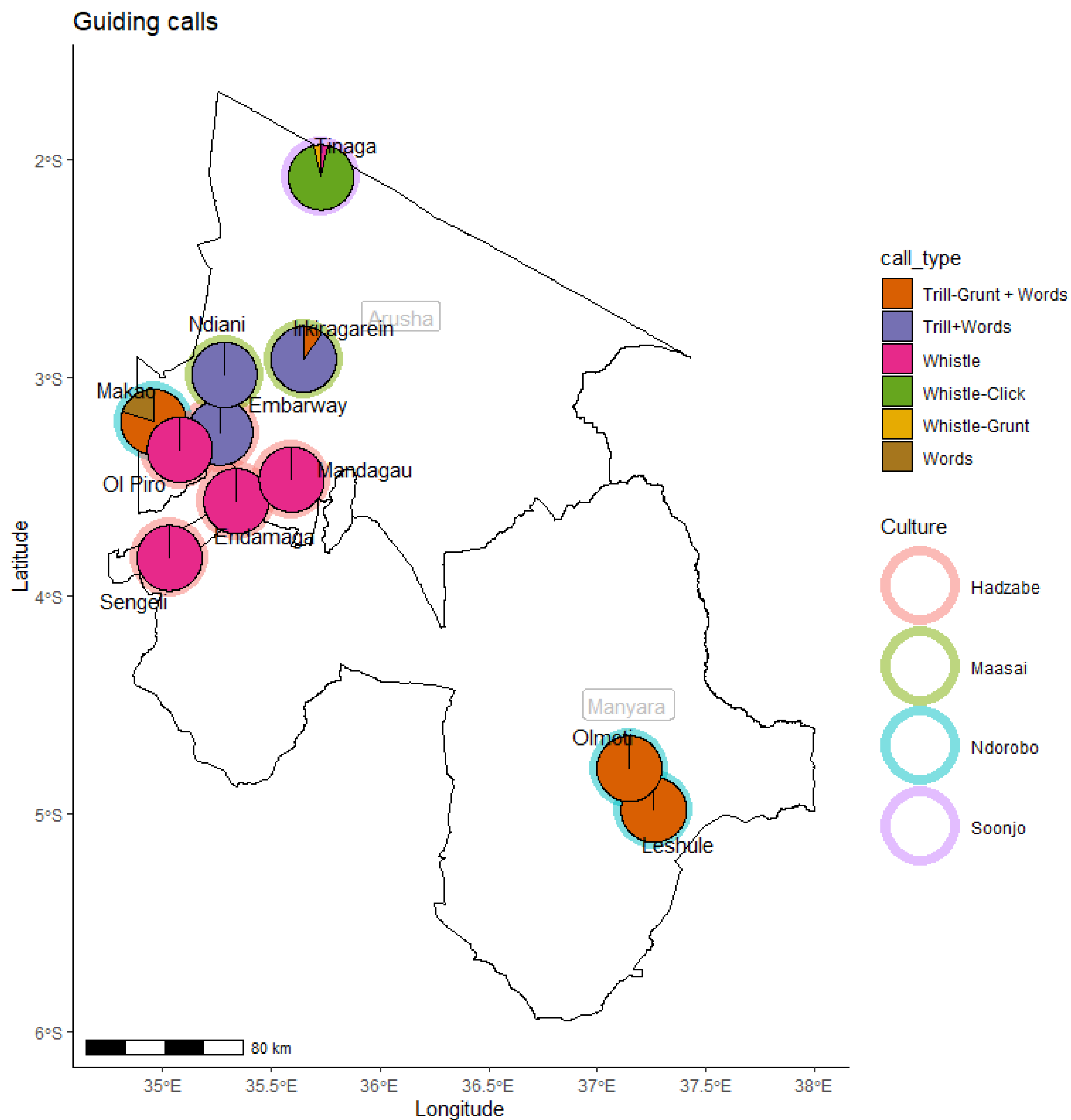

Figure 8 The proportions of different guiding calls that respondents reported they used, per village.

(iii) What are each cultural groups' traditions of rewarding the honeyguide?

(a) What do honey-hunters take from a honeybees' nest for themselves?

Figure 9 shows the bee products taken by honey-hunters for their own use, across the four honey-hunting cultural groups. Overall, the results indicated that people of all four cultures take honey and bee brood for themselves, with only one (3%) respondent mentioning that they take wax for their own use.

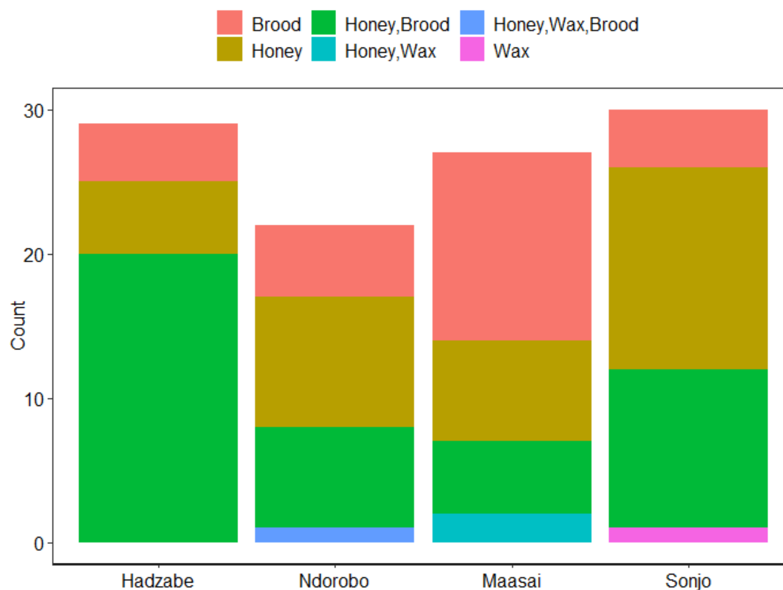

Figure 9: What honey-hunters from the different cultural groups take back home after a honeybees' nest harvest: a mix of brood, wax and honey.

(b) Is rewarding the honeyguide necessary?

100% of the Maasai and Ndorobo subjects said that rewarding of the bird is necessary after being guided to the final bees' nest. Four (14%) out of a total of 29 Hadzabe and four (13%) out of a total of 30 Sonjo subjects responded that rewarding the birds is not necessary. Of the respondents that said that rewarding is not necessary, three explained why: two subjects said that the honeyguide can eat the wax remains on the ground, and one subject explained that this will motivate the bird to guide again.

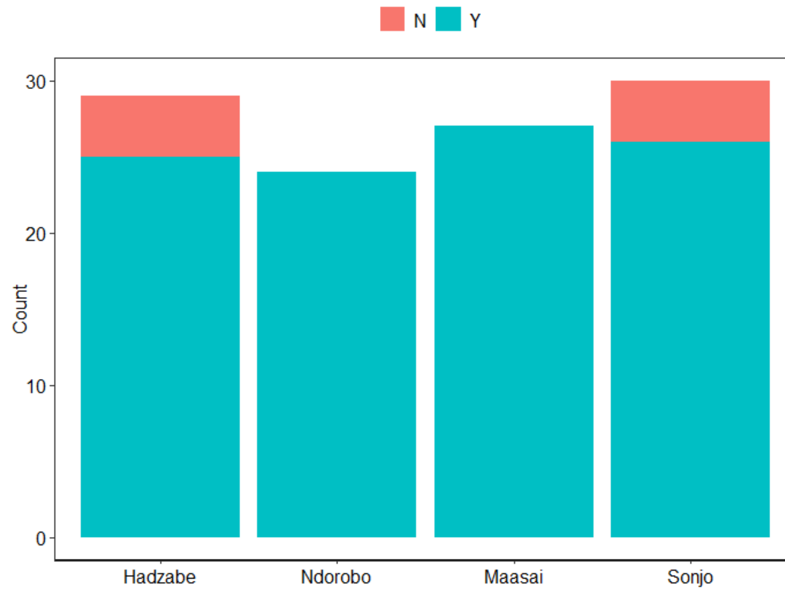

Figure 10: The majority of subjects across cultural groups believed that eventually rewarding the honeyguide is necessary, with the exception of four Hadzabe and four Sonjo subjects.

(c) Why do people reward the honeyguides?

The main reason (58% of Hadzabe, 67% of Ndorobo, 56% of Maasai and 47% of Ndorobo subjects) given why honeyguides need to be eventually rewarded is that the reward is their food (Figure 11). There were also several other reasons mentioned of why they reward among the cultural groups: 21% of subjects said that this ensures the bird keeps guiding, while 24% overall said it is a way to thank the bird for guiding them to a bees' nest. Three Maasai subjects said that rewarding honeyguides with leftovers was little effort as it comes at no cost to the honey-hunter.

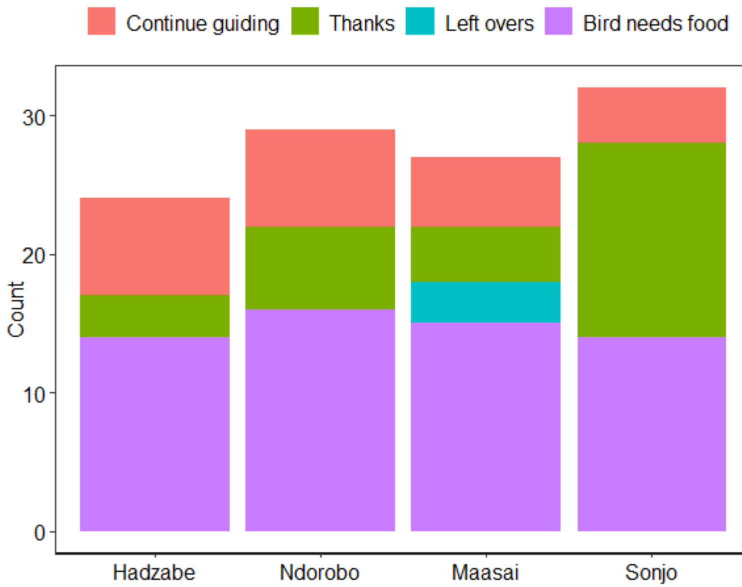

Figure 11: The different reasons given across cultural groups for why subjects reward honeyguides after guiding them to a bees' nest.

(d) With what do honey-hunters reward the bird?

The results indicated that, overall, honey-hunters across all four cultures reward the honeyguide with a mixture of what they find in the contents of bees' nests: bee brood, wax combs, "leftovers" (fragments of wax, sometimes chewed and spat out by honey-hunters), and mixtures of these (Figure 12). The only component consistently reported by all four cultures to be used as reward was bee brood (65% of Hadzabe, 64% of Ndorobo 41% of Maasai, and 88% of Sonjo respondents). From informal interviews with honey-hunters I learned that the amount of wax left behind was relative to the amount harvested: the bigger the harvest, the larger the reward. Honey was not reported to be left as a reward for the honeyguide, except by one Hadzabe respondent.

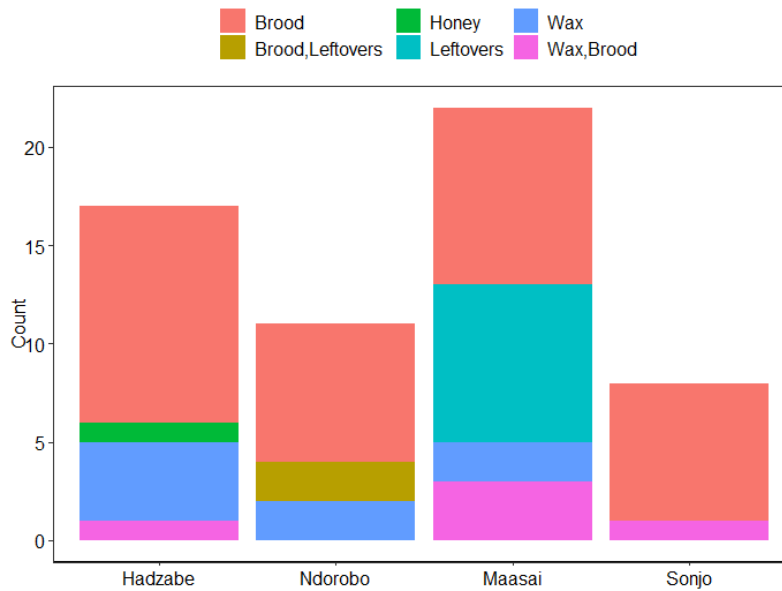

Figure 12: Honey-hunters reported that they use a mixture of bee products as rewards for the honeyguide. Brood is used as the reward by all cultural groups.

(e) Do the honey-hunters withhold the rewards and why?

Many respondents reported that they often withhold (conceal or even burn) the wax, in an effort to avoid the bird getting a reward too soon: 97% of Hadzabe, 75% of Ndorobo, 33% of Maasai and 62% of Sonjo say that they withhold wax from the bird (Figure 13). These percentages significantly differ between cultural groups: Hadzabe respondents withhold significantly more (Fisher's test: $p < 0.001$) than both Maasai (Fisher's pairwise test, $p < 0.001$) and Sonjo (Fisher's pairwise test, $p = 0.01$) respondents, and the Ndorobo respondents withhold significantly more compared to the Maasai (Fisher's pairwise test, $p = 0.02$).

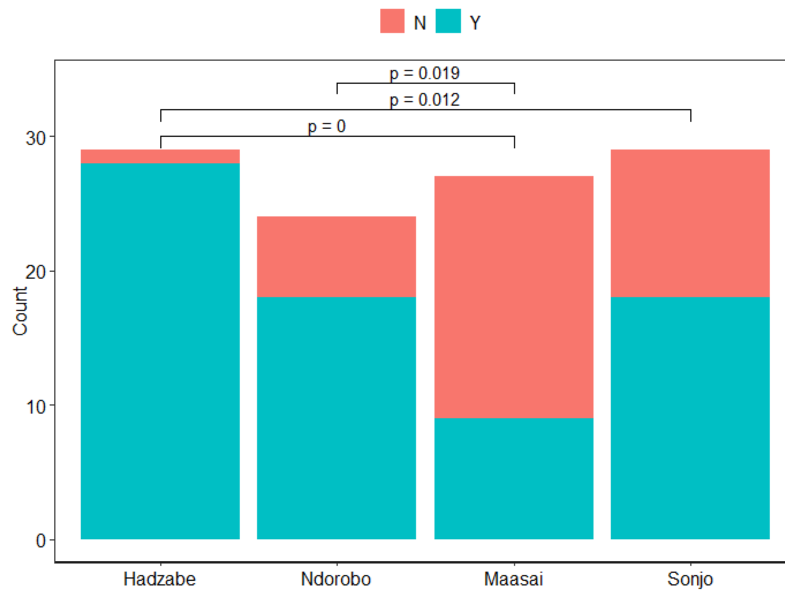

Figure 13: The proportion of subjects that withheld the wax from the birds (or not) per cultural group, and how they significantly vary.

(f) Why do honey-hunters withhold the wax?

Respondents reported that they withhold the reward for different reasons, but the main reason given was that the honeyguide can guide the honey-hunters to other bees' nests (Figure 14). Overall 84% of respondents said that, when you don't reward the birds with wax, it will lead you to another bees' nest (Figure 15). Motivation to do this for the bird is food: it will continue to guide until the human harvest a bees' nest, upon which it will receive its reward. Field observations showed that the Ndorobo have an interesting way of securing multiple bees' nests in one go: after the bird guides them to a first tree with a bees' nest, they pretend they don't see it and keep moving, upon which the bird typically leads them to other bees' nest(s). This is, effectively, trying to cheat the bird.

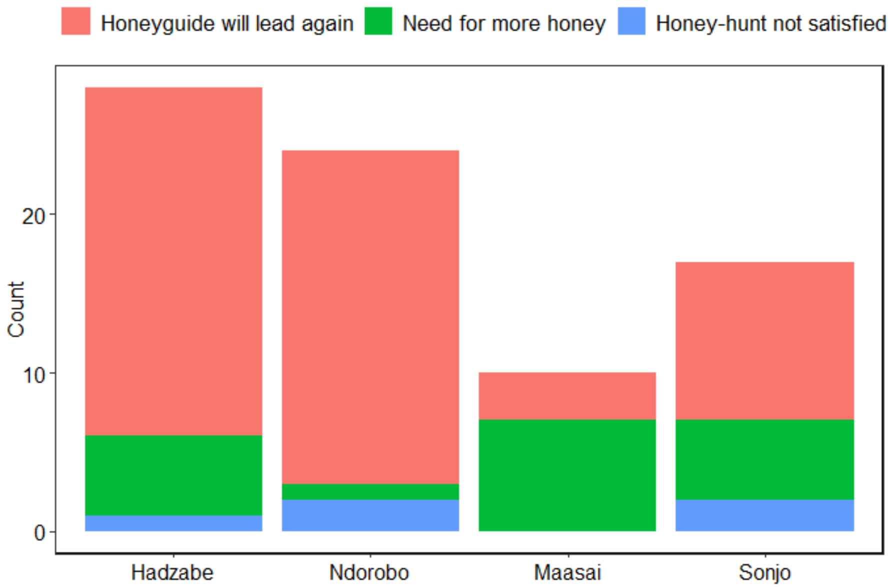

Figure 14: The reasons given per cultural group for withholding the wax reward for the bird.

When asked what happens if you don't reward the honeyguide, the vast majority (84%) of subjects said that it means the bird will continue to lead you to more bees' nest (Figure 15). 13% said that "nothing will happen if you don't reward". One Ndorobo respondent said "the bird will go away". One Sonjo person said "no idea", and a second Sonjo person said "a bad day will happen to you".

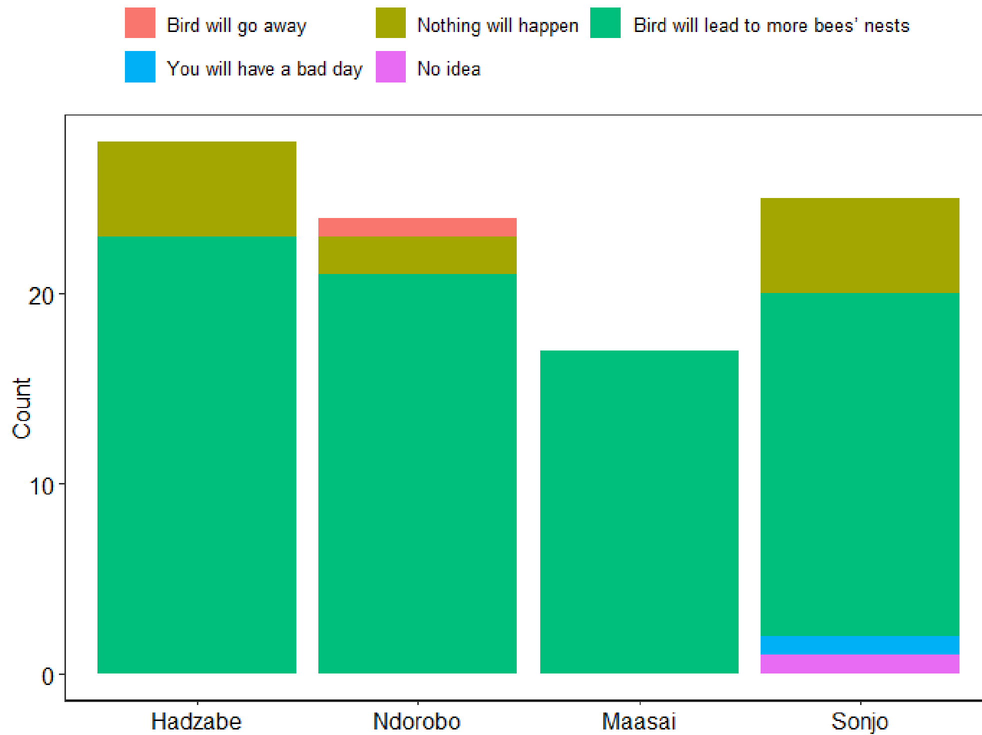

Figure 15: Responses to the consequences of not rewarding the bird.

(iv) What methods do different cultures use to subdue honeybees?

Overall across cultures, smoke from a wood fire was a common method used to subdue honeybees (not measured). Some respondents said they used methods other than smoke to subdue bees (Figure 16), and this proportion of respondents significantly differed between cultures (Fisher's test, $p < 0.001$): significantly more Maasai (66%) and Ndorobo (54%) people used other methods besides smoke, than Hadzabe (3%) and Sonjo (10%) people.

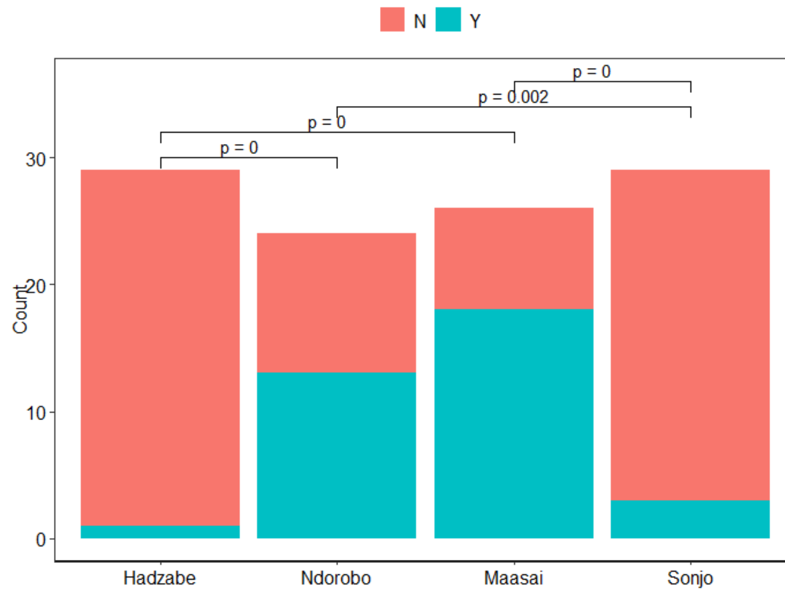

Figure 16: Proportion of respondents who reported that they use other methods besides smoke to subdue honeybees (Y), for each cultural group.

Subjects described four different alternatives to smoke to subdue bees (Figure 17). The main one, used mostly by the Maasai and Ndorobo, was the use of a fungus they called 'Engishimui', used near or in the bees' nests entrance (Figure 18). The 'Engishimui' fungus (subsequently identified from a specimen as *Scleroderma verrucosum*) was reported to be more effective than fire to subdue the bees: its use was demonstrated to me at a beehive, where I observed that honey-hunters use the fungus in two ways (i) by blowing the spores into the bees nest (less preferred method, as it permanently removes the bees from the nest); and (ii) by burning the fungus (more preferred method, since it allows the bees to recolonise the same nest) (Figure 18). I observed that it takes approximately 5–10 minutes after introducing the fungus for the bees to stop flying (Figure 18), and another 30–40 minutes before the bees resume flying. Another method reported by some of the Sonjo is burning a specific plant/herb (not identified) near the bees' nest entrance. Some of the Hadzabe reported that they simply blow air into the bees' nests, while some of the Sonjo reported that they pour water into the bees nest.

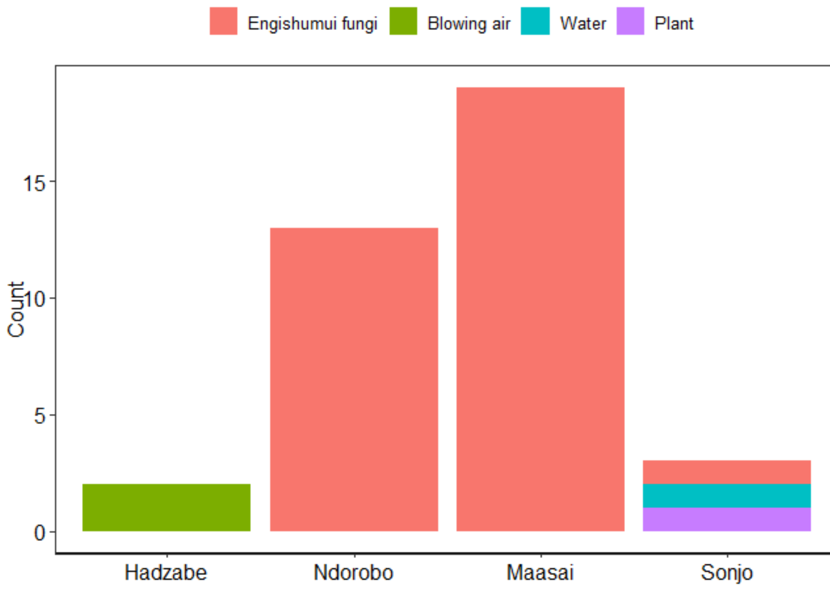

Figure 17: Variation of the different traditional methods used to subdue bees besides the use of smoke among the four cultural groups.

A

B **C**

Figure 18: The fungus called 'Engishimui' (identified as *Scleroderma verrucosum* by Dr Donatha Tibuhwa), used by the Maasai, Ndorobo and (less often) Sonjo people to subdue bees, and the result of its use. (A) The fungus; (B) and (C) bees subdued by smoke from burning the fungus.

(v) What are each cultural group's traditions of ownership of wild bees' nests?

The Ndorobo were the only cultural group in which respondents (71%) said that there was a system of ownership of wild bees' nests; no Hadzabe, Maasai or Sonjo respondents reported that they currently have any ownership system of wild bees' nests, although some Maasai respondents commented that in former times a system of ownership existed, but no longer does. The Ndorobo system of ownership involves people marking trees (using machetes or axes into the trunk) in which they have found a bees' nest, which signals to other honey-hunters that they are forbidden to harvest it. Each honey-hunter has his own personal mark that is different to the marks of other honey-hunters in the village. Of the Ndorobo respondents who said that they marked trees, 22% reported that they frequently revisit their marked bees' nest to make sure it has not been harvested by others.

(vi) What is the future of the mutualism among the four cultural groups?

(a) Do people perceive changes in the mutualism over time?

To understand whether the human-honeyguide mutualism is changing over time, I directly asked honey-hunters whether they perceived any changes in honey-hunter practices from when they were young. Among the respondents, 55% of Hadzabe, 48% of Ndorobo, 78% of Maasai and 67% of Sonjo people said that they have witnessed changes in honey-hunting compared to previous years (Figure 19A). When asked whether they thought the role of the honeyguide in their honey-practices had changed, 35% of Hadzabe, 40% of Maasai, 9% of Ndorobo and 55% of Sonjo (Figure 19B). When asked whether they think that the mutualism will still exist in the future, 21% of Hadzabe, 59% of Maasai, 33% of Ndorobo and 60% of Sonjo subjects responded that they think it will.

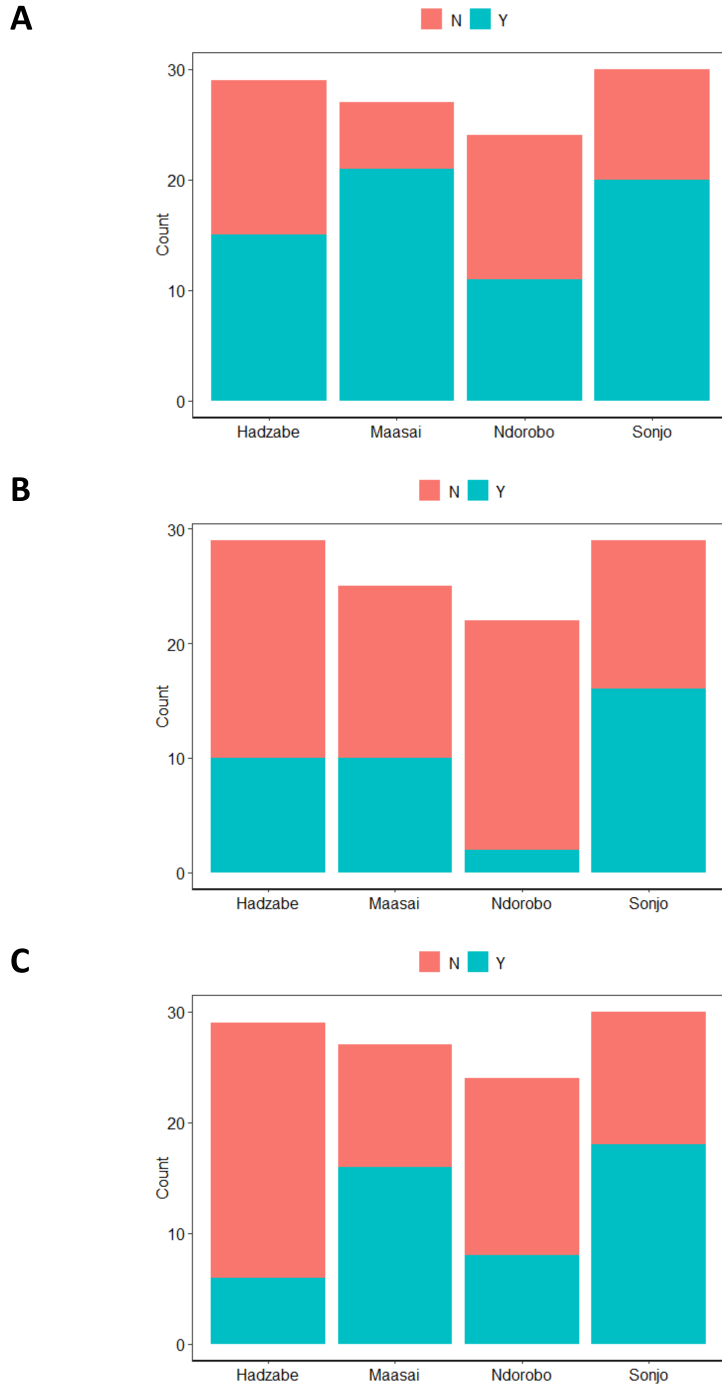

Figure 19 Whether subjects from the 4 honey-hunting cultures perceived: a change in (A) honey-hunting and (B) role of honeyguides compared to previous years, and (C) whether they expect the human-honeyguide relationship will continue to exist in the future.

(b) What reasons do people give for these changes?

The main reasons given for declines in honey-hunting were, first, declines in bees due to climate change-related environmental changes such as reduced rainfall (given by 57% of Hadzabe, 20% of Maasai, 8% of Ndorobo and 13% of Sonjo respondents, for the subset of respondents who reported such changes). Second, declines in bees due to unknown factors (given by 37% of Hadzabe, 32% of Maasai, 33% of Ndorobo and 23% of Sonjo respondents). Third, an increase in pastoralist activities resulting in the decline of bees and flowering plants (given by 7% Hadzabe, 20% of Maasai, 17% of Ndorobo and 21% of Sonjo respondents). Hadzabe and Ndorobo respondents reported dwindling flowering plants and bee colonies, caused by reduced plant species richness caused by intensive grazing, leading to poor colony health. In addition, they reported that excessive cutting down of trees such as *Commiphora africana* (a favored nesting tree for honeybees, (Gandiwa, 2011) for livestock fences and other purposes has resulted in a decline in bees nests in the area. Fourth, an increase in beekeeping (given by 40% of Maasai, 42% of Ndorobo, and 21% of Sonjo respondents). Hadzabe respondents did not mention bee-keeping as an issue, and in the field we observed that beehives in Hadzabe area were derelict. Finally, 8% of Sonjo people reported that 'education and civilization' were a driver of declines in honey-hunting.

The main reasons given for a change in the role of honeyguides in honey-hunting were, first, that fewer people are aware of or have knowledge about honeyguides (given by 22% of Hadzabe, 100% of Maasai, 100% of Ndorobo and 64% of Sonjo respondents, for the subset of respondents who reported such changes). Second, that young people are more educated and no longer interested (given by 33% of Hadzabe and 21% of Sonjo respondents). Third, that pastoralists and agricultural activities mean fewer birds and bees (given by 33% of Hadzabe and 7% of Sonjo respondents), and finally, that there has been an increase in beekeeping via government and NGO schemes (given by 11% of Hadzabe and 7% of Sonjo respondents).

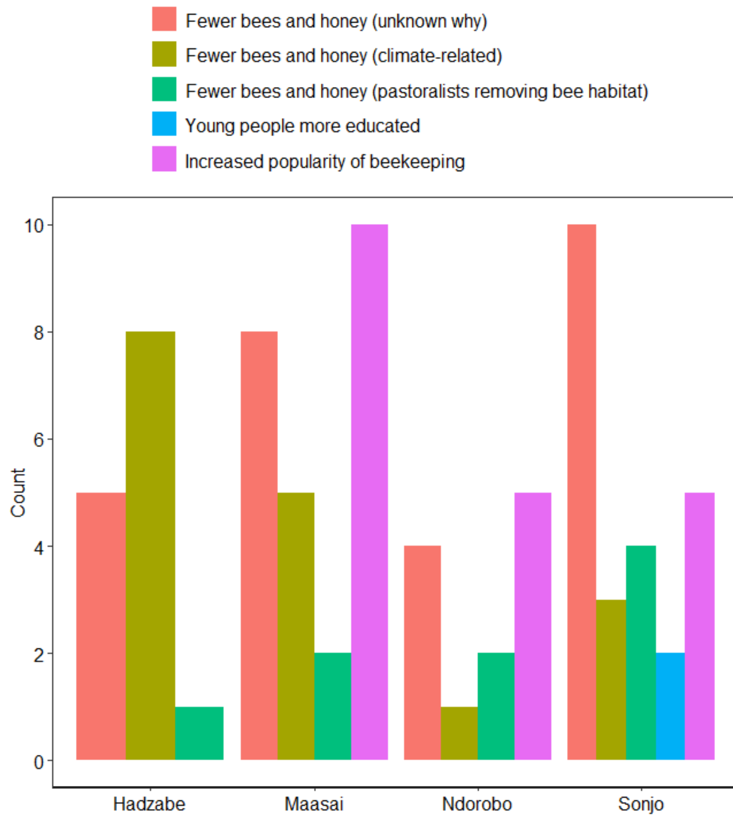

Figure 20 The different reasons respondents give for a change in honey-hunting over time, among different cultural groups. Some people gave multiple reasons, so columns do not sum to 100%.

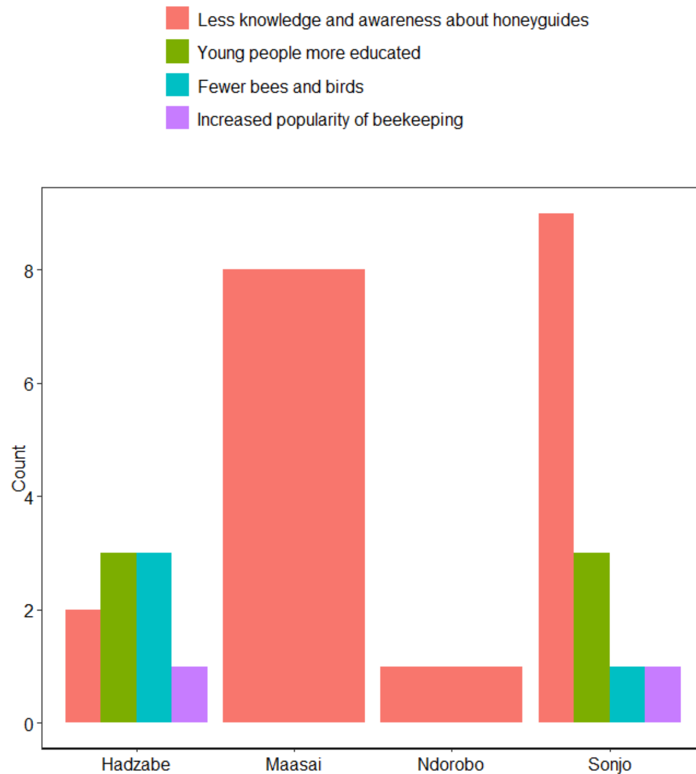

Figure 21 The different reasons respondents give for a change in the role of honeyguides in honey-hunting over time, among different cultural groups. Some people gave multiple reasons, so columns do not sum to 100%.

(c) Is there evidence of a decline in honey-hunting activity?

Figure 19 shows the time (in years) since respondents stated they last went honey-hunting, which gives an indirect picture of how active they are as honey-hunters. The age of last honey-hunt did not significantly differ between cultural groups (GLM, Poisson, χ^2= 2.73, Df = 3, p = 0.44; Figure 19). However, Figure 22 shows that many respondents had not honey-hunted for many years, sometimes up to a decade or more. These inactive honey-hunters might conceal a difference among active honey-hunters. Figure 20 only considers active honey-hunters (defined as respondents have honey-hunted in the last year), and shows that the time since last honey-hunt is significantly shorter for Hadzabe compared to Maasai (GLM, Poisson, $p < 0.001$), Ndorobo ($p = 0.049$) and Sonjo ($p = 0.001$) respondents, and shorter for Ndorobo respondents than for Maasai respondents ($p < 0.001$) (Figure 23). Taken together, this further suggests that Hadzabe

respondents were the most active and frequent honey-hunters, and the Maasai respondents the least active.

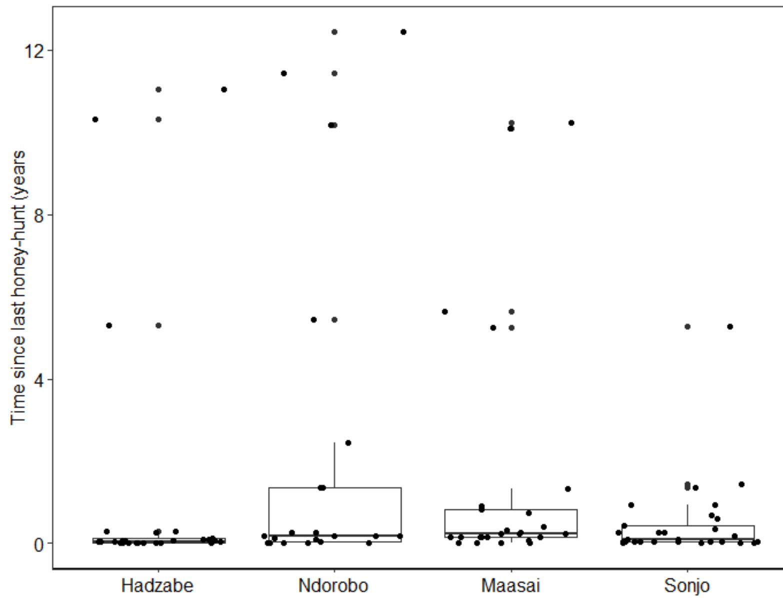

Figure 22: Time since respondents' last honey-hunt for each cultural group, for all honey-hunters. Boxplots indicate the median, quartiles, whiskers (max. 1.5 * inter quartile range), and all individual data points are shown jittered.

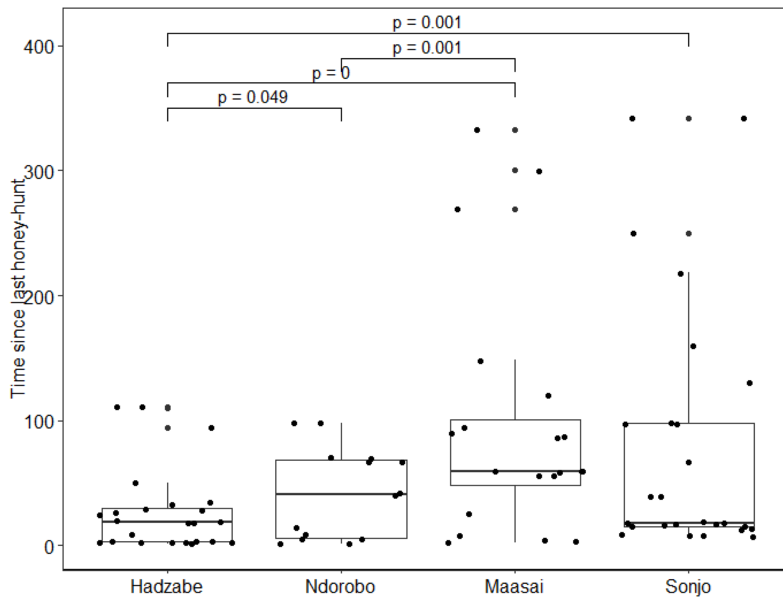

Figure 23: Time since respondents' last honey-hunt for each cultural group, for active honey-hunters only (defined as those who have honey-hunted in the last year). Boxplots indicate the median, quartiles, whiskers (max. 1.5 * inter quartile range), and all individual data points are shown jittered.

Figure 24 shows the current age (in years) of currently active honey-hunters, which gives another indirect picture of how active each culture is as honey-hunters: if young people are no longer becoming honey-hunters, we would expect to see an older population of active honey-hunters. However, the average age of currently active honey-hunters did not significantly vary between cultural groups (GLM, Poisson, $\chi^2 = 0.62$, Df = 3, p = 0.89).

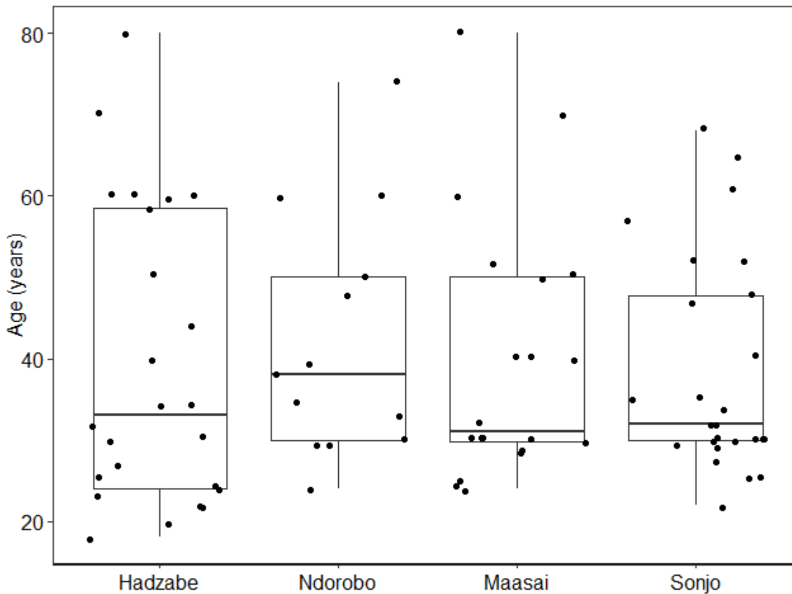

Figure 24: Current age of respondents who are currently active honey-hunters, for each cultural group. Boxplots indicate the median, quartiles, whiskers (max. 1.5 * inter quartile range), and all individual data points are shown jittered.

Finally, Figure 25 shows the age at which respondents reported that they first went honey-hunting. This shows found that Hadzabe respondents first learnt to honey-hunt at a significantly younger age than Sonjo (GLM, Poisson, p = 0.02) and Ndorobo (p = 0.007) respondents.

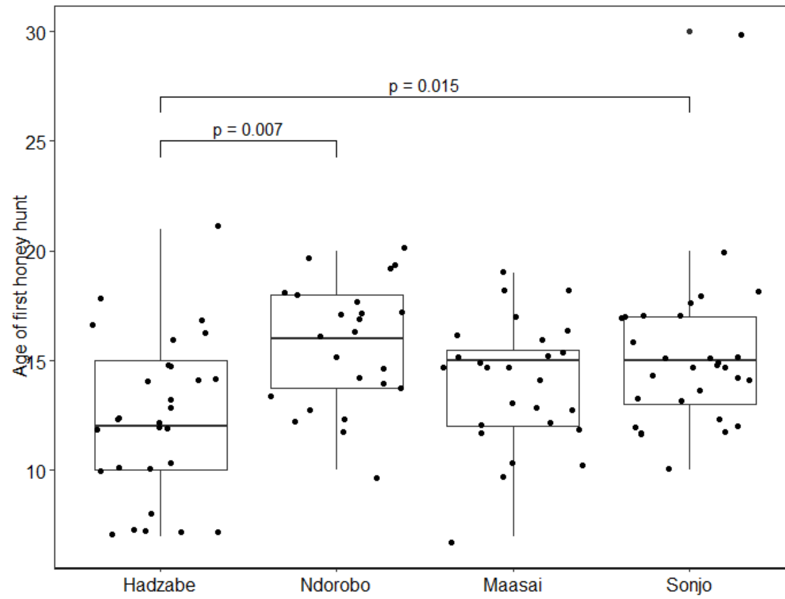

Figure 25: Age at which respondents reported they first went honey-hunting, for each cultural group. Boxplots indicate the median, quartiles, whiskers (max. 1.5 * inter quartile range), and all individual data points are shown jittered.

Discussion

In this study I investigated the honey-consumption and honey-hunting cultures of five coexisting human cultural groups in northern Tanzania, and their relationship with the greater honeyguide. To do so I interviewed 129 people in 12 villages in northern Tanzania, and specifically asked questions relating to the importance of honey in each culture, the calls used to communicate with the birds, the methods used to subdue bees, whether there is any ownership of the bees, and the likely future of the mutualism given cultural changes over time.

I found that honey is an important wild product for all five cultural groups in this region that I sampled, of which four obtain honey themselves rather than buying or trading for it. Honeybee (*Apis mellifera*) honey was the mostly commonly harvested honey type across all cultural groups, but people also use stingless bee honey. The way that honeybee honey is consumed differs among cultural groups (Figure 2A). The Hadzabe and Ndorobo are traditionally considered as hunter-gatherers, and use honey mostly for food and medicine; the pastoralist Datoga use honey for ceremonies and for making local beer; and the pastoralist Maasai and the agropastoralist Sonjo have multiple uses of the honey (food, medicine, beer and for traditional ceremonies). The Datoga are the only cultural group I surveyed that do not honey-hunt: they buy honey from other cultural groups who are specialized honey-hunters (Figure 4). The Hadzabe and Ndorobo get all their honey exclusively from honey-hunting, whereas the Maasai and Sonjo source their honey partly from honey-hunting, and partly from beehives and by buying it from other cultures (Figure 4). Stingless bee honey (which can only be obtained from honey-hunting) was reported to be used as both food and medicine by all five honey-consuming cultures (Figure 2B).

Honey also was reported as an important source of income by the majority of respondents across the four honey-hunting cultural groups (Figure 3). The importance of selling honey depended not only on how much honey people can obtain, but also on how easily they are able to sell it. Ndorobo people in particular commented that they suffer from lack of market

access for honey, such that many Ndorobo people reported that they only go honey-hunting specifically in response to need from themselves and few specific people who require honey from them.

Overall, the market price of honeybee honey is high. The price of a 20 litre container of honey (100,000–150,000 TSH, or approximately US$40–US$65) is equivalent to 10–15 days' work at the standard basic wage. However, if instead bartered for livestock, this same 20 litres can be exchanged for one cattle calf which has a value of 300,000 TSH. Honey-hunters therefore typically prefer to exchange honey for livestock rather than selling it for cash. The market price of stingless bee honey (which is lower yielding per nest and typically not harvested with the help of honeyguides in this region) is several times higher than this. This is a clear motivation for honey-hunters to go honey-hunting, particularly given that stingless bees are not kept in man-made beehives.

Although respondents reported an increase in beekeeping among several cultural groups, particularly the Maasai and Sonjo, honey-hunting still remains important to the community as a whole. Many people commented that they find themselves turning back to wild bees' honey rather than honey from beekeeping, as it is believed that wild bees' honey (from both honeybees and stingless bees) has a high concentration of pollen from natural plants or herbs which can heal different diseases to honey from beehives. Similarly, some cultural groups such as the Maasai who use wild honey for blessing people in ceremonies prefer that this honey is collected from wild bees through honey-hunting. This demand specifically for wild-harvested honey at markets may partly explain why honey-hunting continues to be important despite the spread of beekeeping, and with it the use of honeyguides.

Does human-honeyguide communication vary across cultures?

In sub-Saharan Africa, different honey-hunting cultures have developed their own calls to attract honeyguides and to communicate with them while following them (Isack & Reyer, 1989, Wood *et al.*, 2014, Spottiswoode *et al.*, 2016). In this study I compared the calls used in the different

villages I surveyed, across those four cultures that practice honey-hunting and so depend on honeyguides. Like in some other studies (Honeyguide Research Project, unpubl. data), I found that many of the subjects in my study reported that they use somewhat different calls for the two phases of a honey-hunt: first to attract the honeyguide (referred to here as 'attracting calls'), and then to maintain their attention while following honeyguides ('guiding calls'). I found that different cultural groups have different calls to communicate with honeyguides, and that these calls were highly consistent both within villages and across different villages of the same cultural group, even when these were geographically far from one another (e.g. attracting calls and most guiding calls for Ndorobo people in Makao vs. Olmoti and Leshule, about 300 km apart) (Figures 7 and 8).

First, Hadzabe respondents reported that they used either melodious whistles (Sengeli village) or spoken words or a combination of melodious whistles and words (Endamaga, Olpiro and Mandagau villages) as attracting calls, whereas all Hadzabe respondents without exception stated that they use melodious whistles as guiding calls. Second, all Ndorobo respondents stated that they use a use "trill-grunts" as attracting calls, and either a mixture of "trill-grunts" and words, or in a few cases at Makao village only words, as the guiding calls. These trill-grunts are remarkable for sounding very similar to the "brrr-hm" trill-grunt calls used by Yao honey-hunters 1,000 km away in the Niassa region of northern Mozambique (Spottiswoode *et al.*, 2016). Third, Maasai respondents also largely reported using similar "trill-grunts" mixed with words, or in a few cases just "trills" and words, as both attracting and guiding calls. However, the exact words used differed between attracting and guiding calls, as explained in the next section. Finally, Sonjo respondents reported using mostly simple whistles (the same note repeated several times, rather than the Hadzabe whistled melody, and in a few cases mixed with "grunts" or "clicks") as attracting calls, and mostly used similar whistles mixed with clicks as guiding calls. The similarity between Maasai and Ndorobo honey-hunting calls (variations on "trill-grunts" in both cultures, mixed with words particularly for the Maasai) probably reflects the fact that the Ndorobo hunter-gatherers and have lived with and been dominated by the Maasai pastoralists for many years. This is also reflected by the similar meaning of the words used, as explained in the next section.

When people use words from their own language to attract the bird or to communicate with it when it is guiding them, the meaning is often to express their humble feeling to the honeyguide who knows the location of the honey. For example, Maasai respondents reported using simple words ("*enjarwatai"*, meaning "sheep") mixed with trill-grunts when attracting honeyguides. But when a honeyguide starts to guide them, they then switch to more complex messages interspersed among trill-grunts (transcribed here as "*Prrr, Hii*") as guiding calls, such as *"Prrr, Hii, Prrr, Hiii, enjarwatai, Prrr, Hii, Prrr, Hiii, looto, lemulugulu, lendonata, prrr, hii, tulimu*" which approximately means "Please my dear sheep, please show me the location of the honey, I can harvest it while I am kneeling or standing from the tree or from the termite mound, but please don't lead me to a dangerous animal". The word "my sheep" is to glorify the bird; this is because the oil extracted from the tails of slaughtered sheep looks similar in colour to honey, and is given to women giving birth or to reconcile people who are in conflict. The honeyguide is therefore considered as the sheep that shows honey, since the honey and sheep-tail oil not only look alike, but have similar problem-solving functions, since both are used to reconcile people who are in the conflict and used for blessings and as the dowry during the marriage season.

Similarly, words used by the Ndorobo respondents adopted some Maasai words like "enjarwatai" ("sheep"), and broadly had a similar meaning such as "my love, show me the honey from the tree or from the mound". This again probably reflects the cultural transmission that has occurred from Maasai to Ndorobo people, who are often employed by Maasai people and have adopted many Maasai cultural traditions (Distefano, 1990). Words that Hadzabe respondents reported they used included "*Hoe, Hoe, tikiliee, hoe, bachoe, hamana, thohakwasa, bushoekuwasa*", meaning "honeyguide, please come and take me, I am feeling hungry come, I am here, come and take me to the honey".

This variation among the cultural groups in words directed at honeyguides therefore appears to reflect the main use of the honey: Hadzabe respondents ask the honeyguide to show them honey because they feel hungry and they need something to eat, while the Maasai call the

honeyguide a sheep because they compare honey to the valuable products of a sheep, used for reconciliation or for ceremonies.

In parts of the Ngorongoro area, people of more than one culture honey-hunt in the same area and are likely to meet the same individual honeyguides. For example, the Embarway area is used by both Maasai and Hadzabe people for honey-hunting. Both Maasai and Hadzabe people report that they incorporate words into their attracting calls (as well as trill-grunts for the Maasai and whistles for the Hadzabe), which we could speculate may enable honeyguides to recognize honey-hunters of both cultures in places where they mix. After the bird has begun guiding, the human calls then differ, with Maasai people mixing trills and words, and Hadzabe people giving solely whistles. It would be interesting to know whether honeyguides are more likely to persist in guiding people who switch to whistles at this point, since that would signal that the person is more likely to be an expert honey-hunter and eventually be associated with a reward. Finally, it would also be very interesting to know why Ndorobo and Maasai share such similar "trill-grunt" honey-hunting calls to the Yao people of northern Mozambique (Spottiswoode *et al.*, 2016). This is particularly interesting because Yao people speak a Bantu language and are not closely related to the Maasai or Ndorobo people who are of Nilotic origin.

Do cultures differ in their traditions of rewarding the honeyguide?

The interest of honeyguides in the contents of the bees' nest is particularly in the beeswax and the bee brood. In some places in Africa, the honey-hunters reward the birds with wax and/or brood as a sign of gratitude, and to motivate the birds to leads them again (Isack and Reyer, 1989). However, in other cultural groups such as the Hadzabe, people have been documented to burn or bury the wax, which they report functions to keep the honeyguide hungry so that it can guide them to another bees' nest (Wood *et al.*, 2014).

During my study, in northern Tanzania, I found that all four cultural groups have strikingly different traditions of whether and when to reward the birds. Overall, the bee products left for the birds (wax and brood) are largely those not used by many honey-hunters themselves –

although humans also consume brood (Figure 9) – so at first sight it should not be costly to allow the birds to eat them. However, respondents from some cultures, particularly nearly all Hadzabe respondents (Figure 13), nonetheless actively prevent the honeyguide from eating these products by concealing or burning them, which they reported they do so the bird still feels hungry and leads them to other beehives, similar to previous reports (Wood *et al.*, 2014). Interestingly, Ndorobo respondents verbally reported that they use a slightly different strategy to withhold the wax, whereby, they try to "cheat" the bird by pretending they haven't seen the bees' nest that a bird has shown them, and so do not harvested it yet, but keep moving forward so that the bird continues and leads them to another bees' nest. I also witnessed this personally on both Ndorobo honey-hunting trips I accompanied where we were guided by a honeyguide. Only when the bird has shown the Ndorobo honey-hunters more than four nests do they harvest one or more nests and reward the bird, and will later the same day return to harvest the nests that they earlier ignored. A similar strategy has been previously reported from Boran honey-hunters in Kenya (Isack 1999).

Some Maasai respondents also reported that they sometimes actively conceal the reward until their honey-collecting bucket is full, whereupon they reward the bird. Other Maasai respondents reported that they do not actively provide a reward, and instead leave the honeyguide to come and eat leftovers from the ground. Many Maasai were also beekeepers, which may explain why they seem less concerned about the bird not showing them more bees' nests.

Overall, it is striking that respondents had a generally positive view of the consequences of not rewarding the bird (Figure 15). Most (84% across all cultures) said it is beneficial because it encourages the bird to show you more bees' nests; 13% were neutral and only two people suggested negative consequences of depriving the bird ("the bird will go away" or "you will have a bad day"). This positive view is also consistent with the fact that honeyguides clearly still guide people in spite of being often deprived of wax, since the mutualism still thrives in this region. Perhaps this is because honeyguides ultimately obtain enough wax from an eventual harvest and

reward after several bees' nests have been shown (as practiced particularly by Ndorobo people and to a lesser extent Maasai people).

This positive view of depriving the bird contrasts with the traditions of many other cultural groups elsewhere in Africa who have been documented to report negative consequences of failing to reward the bird, such as "punishment" through being shown dangerous animals instead of bees (Friedmann, 1955). While many of the words used by humans to communicate with honeyguides indicate that people do not wish to be shown dangerous animals instead of honey (see previous section), these results suggest that such honeyguide behaviour is not interpreted as punishment for failing to leave it wax, unlike in some other cultures (e.g. Friedmann, 1955).

Do cultures differ in the methods they use to subdue stinging honeybees?

The defensive behavior of honeybee colonies has been advantageous for the evolution and ecological success of honeybees but is a disadvantage for honey-hunters. Honey-hunters have found several different solutions to the problem of how to avoid being stung by honeybees. The use of smoke from wood fire to subdue the bees has been used for many years and is an effective way of calming the bees and reducing their stings to the honey-hunters, but also has negative effects on the bees by causing them stress and sometimes by sparking wildfire (Joshi and Gurung, 2005). My interviews showed that people can still extract quality honey from wild bees using alternative traditional methods to the use of fire (Figure 16), which respondents stated have fewer negative effects on the bees and their habitat.

Specifically, the Maasai and the Ndorobo (and rarely the Sonjo) reported that they often use a fungus (mushroom) traditionally known as 'Engishimui' to subdue the bees (Figures 17, 18). This has fewer negative effects on the bees when burned to produce smoke rather than when used unburnt, and so burning is preferred, since this reportedly increases the chance that the bees will recolonize the nest. The 'Engishimui' fungus was kindly identified as *Scleroderma verrucosum* by Dr Donatha Tibuhwa at the University of Dar es Salaam, from a specimen I provided. This species has not been previously reported as a bee pacifier in published lists of plants and fungi used for this purpose (Crane, 1999, Kraft and Venkataraman, 2015, Tibuhwa

2012). Another fungus species used in Tanzania to subdue bees, *Langermannia wahlbergi* (= *Calvatia argentea*), has been shown to produce hydrogen cyanide when burnt (Wood 1983). This subdues the bees apparently without affecting their survival, as reported for *Scleroderma verrucosum* by the honey-hunters I interviewed.

Remarkably, when I accompanied Hadzabe and Ndorobo people on honey-hunts, I witnessed that they sometimes did not use any method to subdue the bees when harvesting their honey. People were able to predict the defensive behavior of the bees by looking the type of the tree in which the bees' nest is located, allowing them to predict the bees' level of aggression and so to decide whether or not fire or other methods are required. If not, they may harvest their honey using their bare hands. Specifically, *Commiphora africana* is one such common honeybee nesting tree where I personally observed honey-hunters harvesting honeybee honey without the use of the fire or any other method to subdue bees. Bees nesting in large bulbous trees such as baobabs (*Adansonia digitata*) or other large flowering trees are known to be aggressive, and so require fire or others methods to subdue them. By contrast, Maasai and Sonjo people seemed warier of bees and always used methods (fungi or smoke) to subdue them.

Taken together, these findings suggest that honey-hunters take care to use less destructive harvesting methods when possible given the aggression levels of the bees that may encourage the bees to recolonize the harvested nest.

Do cultures differ in their systems of ownership of wild honeybees' nests?

Bees and humans have probably interacted for many years, as human ancestors probably did given that chimpanzees modify the branches of trees into specific tools to probe instead bees' nests to access of the honey (Bradbear, 2009). Ownership of wild bees' nests, as reported by Ndorobo people (but currently none of the other cultures I interviewed), is probably a more recent development. Such ownership of free-living animals is unusual, especially for wild bees rather than bees nesting in man-made hives. The majority of honey-hunters of the Ndorobo

communities I interviewed had a bees' nest in a tree in which he has put his mark, which is recognized by other honey-hunters and also by the villagers in general. Analogous systems of marking 'owned' wild bees' nests have been reported from for example Mali, Djibouti and South Africa (reviewed by Crane, 1999). Ndorobo subjects reported that harvesting honey from such a bee colony that is not yours, because you are not the first to discover it, is taken as an illegal offense and the offending person should be punished by the laws applied by that culture. Honey-hunters will take a person who has illegally harvested someone's honey to the traditional leaders to provide such a punishment, if they can prove that he has harvested the honey that is not his own. A similar system of ownership was also previously in existence in Maasai culture, but some respondents explained this has disappeared from generation to generation due to cultural changes, including reduced respect for their traditional leaders. This is potentially important for the sustainability of honey-hunting, given that ownership should give an incentive for sustainable harvesting to ensure future harvests of the same nest.

What does the future hold for the human-honeyguide mutualism in northern Tanzania?

The relationship between honeyguides and people is likely to have existed for many years, maybe even hundreds of thousands of years (Wrangham, 2012). However, the relationship is likely to change through space and time. There are concerns that honeyguides will stop guiding humans to bees' nests, if people reduce the payoff to honeyguides by not following them (e.g. Isack, 1999). In my study, I found that cultural leaders commented that people are likely to change their behavior of following the honeyguide, but that honeyguide behavior will continue to exist because the birds' cooperative behavior is innate and honeyguides will continue to be born with that behaviour, whereas the cooperative behaviour of humans is learned and so may disappear over time.

In some cultures, bee-keeping appears to have taken the place of honey-hunting and was reported to be a driver behind peoples' reduced interest in honeyguides. In particular, the Maasai and the Sonjo did not appear to be particularly active honey-hunters, and also were the only two cultures to report practicing beekeeping. This also reflects that they are not hunter-gatherers but

instead pastoralists and agro-pastoralists, respectively, so are accustomed to looking after domesticated animals, which is culturally closer to bee-keeping.

By contrast, the Hadzabe and the Ndorobo are still very active honey-hunters. Traditionally these cultural groups subsist from hunting and gathering for their food, rather than tending livestock or growing crops. However, responses indicated that the Hadzabe and the Ndorobo are going through a very difficult time with respect to honey-hunting, which may reduce their effectiveness at honey-hunting in future. In particular, they pointed to the effects of climate change on bee habitat, and to an increase in agricultural and pastoralist activities in other cultures living nearby honey-hunters, which is affecting habitat quality through uncontrolled fire and through the cutting down of trees for expansion of livestock fencing.

In conclusion, my results show that the mutualism between humans and honeyguides is still thriving in this part of northern Tanzania, but this is mostly due to the Hadzabe and the Ndorobo cultural groups who still practice little to no beekeeping. While the Tanzanian government motivates people to practice beekeeping, I suggest that honey-hunting should continue to be permitted since it remains an important source of food and income for honey-hunters, as well as being important for honey consumers who still demand honey from wild bees, as it is believed to cure different diseases and to be more appropriate for ceremonial use than honey from beekeeping. I further suggest that this interaction between wild animals and humans is important as it reduces human-wildlife conflict and makes the community feel part of their ecosystems and invested in their conservation, which is important in this region that is facing so much human impact. The different ways that honey-hunters have devised to subdue bees in ways that have less ecosystem impact than using fire (like the use of the 'Engishimui' fungus that reduces bee desertion) probably reflect peoples' long-term interest in conserving bee populations and so, indirectly, also benefit the honeyguides they cooperate with.

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Appendix 1

The interview questions asked in this study. In grey I've highlighted the questions of which the answers are not discussed in this thesis.

PART 1

A. PERSONAL PARTICULARS

- Name
- Age
- Sex
- Cultural group
- Number of children
- Number of wives
- Born where
- What have you done in the last 12 months to make money?
- Do you use honeybee honey? Y/N
- If yes, what do you use honeybee honey for? (can select more than one) Food/Alcohol/Ceremonies/Medicine/other
- Where do you get your honeybee honey? (Can select more than one) Wild bees/man-made beehives/buy
- What is the market price for honeybee honey in your village
- Do you use stingless bee honey?
- If yes, what do you use stingless bee honey for? (can tick more than one) Food/Alcohol/Ceremonies/Medicine/Other
- Where do you get your stingless bee honey? (Can select more than one) Collect from wild bees/ Collect from own man-made beehives/Buy or trade
- What is the market price for stingless bee honey in your village?
- Do you know the bird that guides people to honeybees' nests? Y/N
- What is the name of this bird in your language?
- Has this bird ever tried to guide you? Y/N

If person collects honey from wild bees – go to **PART 2**

If person collects honey from own man-made hives – go to **PART 3**

If person buys or trades for honey – go to **PART 4**

PART 2 (for people who are honey-hunters)

B. HONEY HUNTING EXPERIENCE

- Where did you to learn honey-hunt?

- At what age did you go on your first honey-hunt? (age or year)
- When was the last time you went on a honey hunt? (age, or month & year)
- What are the best three months of the year for honey hunting?
- How often (per month) do you go honey hunting in the honey hunting high season?
- Do you go on trips only for honey-hunting, or do you mainly honey-hunt opportunistically while busy with other activities like herding cattle? Trips only for honey-hunting/ honey-hunt opportunistically during other activities
- How important is selling honey and/or wax for you as a source of income in the honey hunting high season? Not important, I do not sell/ A little important/ Very important
- When you are out honey-hunting, do you make use of the bird to find bees' nests? Y/N
- How often do you rely on honeyguides to find bees' nest for harvesting? Always/Most often/Sometimes/Never

C. BEHAVIOR

- When you harvest a wild bees' nest, what do you use from the harvest? (can be more than one) Honey/Wax/Brood (or combination)
- Do you ever leave things for the bird to eat after being guided to a bees' nest? Y/N
- If Yes, why?
- If Yes: How much and what? Wax combs or just scraps/spit-out bits of wax? Do you do anything special with what you leave behind?
- Have you ever decided to conceal or burn the wax after being guided? Y/N
- Why or why not?
- What happens if/when you do not reward the honeyguide with wax?
- Have you ever been guided to a man-made beehive? Y/N
- Have you ever been guided to anything else besides bees? Y/N
- If yes, what?
- Why do you think the honeyguide *guided* you to these things, rather than you just coincidentally encountering them, while looking for the bees' nest?
- Have you ever guided by a honeyguide to a nest of a stingless bee?
- When a bird guides you to a stingless bees' nest, do you usually harvest the nest?
- When a bird guides you to a stingless bees' nest, do you usually leave a reward for the bird? Why?
- What is the name of the stingless bees in your local language? (can be more than one)

C. SIGNALS

- Do you use sounds to communicate with the honeyguide? Y/N
- Is this a specific and consistent sound(s) (e.g. particular melody) or is it a generic sound (e.g. any whistle or loud noise works)?
- If specific sound, what kind of sound? (make recordings)
- Do you use this sound for anything else besides communicating with honeyguides? Y?N
- If yes, what for?

- Does the sound you use differ when you are calling in the bird, to when the bird has arrived, and you are following it? Y/N
- If yes, how does it differ?
- From whom did you learn this sound to communicate with the bird? Father/Brother/Uncle/Friend/other

D. SUSTAINABILITY

- Do you have any other means to subdue the bees from stinging than use of smoke? Y/N
- When you harvest a nest, do you do anything to encourage the bees to return to it? Avoid using fire to subdue the bees/ Avoid chopping tree down when possible/ Make a small hole in the tree/ Leave some wax combs behind/ Put a rock or piece of wood afterwards to close the hole/ Give a blessing afterwards/ Other
- If you found a wild bees nest, but then you inspect it and decide that it has not yet been filled with honey and is not 'ready' to be harvested, is there any way you can prevent someone else from harvesting that nest? Or is there no way to control who is allowed to harvest the nest? Possible to prevent another person from harvesting / Cannot control who harvests the nest. If possible to prevent another person, how?
- If it is possible to prevent another person from harvesting: what would happen if you discovered someone had harvested the honey from a wild bees' nest you had found?
- What would happen to the person who did so, if caught?

E. TREND OF MUTUAL INTERACTION IN FUTURE

- Has the practice of honey-hunting in general changed since you were young? Y/N
- If Yes, how has it changed and what is the reason?
- Has in particular the role of honeyguides in honey-hunting changed over time? Y/N
- If Yes, how has it changed and what is the reason?
- Is honeybee honey-hunting considered to be men's work, or the work of both men and women? What about stingless bee honey-hunting? And beekeeping? Why so?
- How many siblings do you have? What are their ages and gender? Do any of them honey-hunt?
- What are the gender and ages of your children? Do any of them honey-hunt?
- Are you keen to teach any member of your Family about honey hunting?
- If Yes, which member would you like to teach? If No, why?
- Do you think the interaction between people and honeyguides will exist in the future? Y/N
- How do you see the interaction between people and honeyguides changing in future generations?

QUESTIONNAIRE PART 3 (for people who keep bees)

- Why don't you collect honey from wild bees? Not enough wild bees around where I live/ Not enough honeyguides around where I live / I am frightened of wild bees / don't know how to harvest them / Easier to keep bees in beehives instead / Other (give details)
- How many of each of these types of bee-hives do you have? Bark cylinder/ Solid wood cylinder, box hive, Other
- What motivates you to keep bees? To collect honey for food / To collect honey for ceremonies / To collect honey to sell / Alcohol / Ceremonies / Medicine / Other (give details)
- From whom did you learn to keep bees?
- When you harvest a man-made hive, do you have any other means to subdue the bees from sting than use of smoke? Y/N
- If yes, what is the other means?
- When you harvest a man-made hive, what do you use from the harvest? (can be more than one) Honey/wax/brood
- When you harvest a man-made hive, do you leave wax or brood behind? Y/N
- What would happen if you discovered someone had harvested the honey from one of your man-made beehives?
- What would happen to the person who did so, if caught?
- Is honeybee honey-hunting considered to be men's work, or the work of both men and women? What about stingless bee honey-hunting? And beekeeping? Why so?
- Do you think the interaction between people and honeyguides will exist in the future? Y/N
- How do you see the interaction between people and honeyguides changing in future generations?

PART 4 (for people who buy or trade honey)

- Why don't you collect honey from wild bees? Not enough wild bees around where I live / Not enough honeyguides around where I live / I am frightened of bees / don't know how to harvest them / Easier to keep bees in beehives instead / Easier to trade for honey instead / Other (give details)
- Why don't you keep bees in man-made beehives? Not enough wild bees around where I live / I am frightened of bees / don't know how to harvest them / Cannot make or afford beehives / Easier to trade for honey instead / Other (give details)
- How do you pay for honey? (can state more than one) Cash money / Livestock / Meat / Crops / Household goods / Other (give details)
- Is honeybee honey-hunting considered to be men's work, or the work of both men and women? What about stingless bee honey-hunting? And beekeeping? Why so?
- Do you think the interaction between people and honeyguides will exist in the future? Y/N
- How do you see the interaction between people and honeyguides changing in future generations?

Appendix 2

Consent script signed by all study subjects

You are invited to participate in a research study that is interested to find out more about how people obtain honey in the Ngorongoro region. If you are a honey-hunter, or a bee-keeper, or obtain honey from other sources, we would like to talk to you. The interview will take approximately one hour, during which you will be asked to answer a set of questions about your relationship with honey and bees. We will also ask you to demonstrate sounds you might make when searching for bees' nests, which we will record. We will audio record the interviews, and may take photographs or record video as part of the study. If you object to this, please indicate this below. If you are an active honey-hunter, we might ask to join you on a real-time honey-hunt during which we will record video and sound, and you are free to accept or decline. Your participation in the above is completely voluntary; you may refuse to participate, and you may withdraw at any time. Should you choose to withdraw, the researcher will not use any of the information you have provided without your signed consent. Note that the researcher may also withdraw you from the study at any time. All information collected in this study will be kept private in that you will not be identified by name. You are free to ask questions or request further information, at any time during this research. There are no potentially harmful risks related to your participation in this study.

By signing or making a thumbprint on this consent form, you agree:

- to participate in this research study
- to be audio-recorded for the duration of the interview
- to be video- and audio-recorded for the duration of the honey-hunt (if applicable)
- to the use of properly anonymized photographs/videos in websites and publications for research purposes

____________________	____________________	________
Name of Participant	Signature or Fingerprint of Participant	Date
____________________	____________________	________
Name of Researcher	Signature of Researcher	Date
____________________	____________________	
Village		