Mutualism between honeyguides, beekeepers and honey-hunters in southern Tanzania

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MSc thesis

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Acknowledgements

Throughout this project, I have received great support and assistance. First and foremost, many thanks go to my great and best supervisors in the world, Prof. Claire Spottiswoode and Dr Jessica van der Wal, for the tireless and incredible support from the beginning of the project until the due date: from formulating research questions, designing data collection protocol, data visualization and analysis, visiting Tanzania for assessing the project writing, and extremely good feedback to push me to sharpen my research knowledge. I want to thank them for inviting me into the incredible "African Honeyguide Project" and it gave me much hope that some good people still exist in the world. I want to say thanks to myself for the hard work and confidence to conduct this project. Finally, I would like to thank my best friend Eliupendo Alaitetei Laltaika for his commitment to drive me to the field and help to get access to the National Parks.

I thank the University of Cape Town, Tanzania Wildlife Research Institute (TAWIRI) and the Tanzania Commission for Science and Technology (COSTECH) for supplying me with the necessary ethics permissions and research permit that allowed me to conduct my field work in southern Tanzania.

Thanks go to my research assistant Paulo Mkata for the help and incredible support during data collection and bees' identification. Thank you to David Lloyd-Jones for guidance in the planning of fieldwork in the Iringa Region. Thanks to Matei Makutiani, and all beekeepers in the beekeeping camps for the incredible help during data collection.

I'm very grateful to my generous friends Adair Dammann, Danferd Henke, Stephanie Van Dyke, and Yarrow Durbin, who together have made it possible to attend this MSc course: my first dream is achieved.

Thanks to Prof. Claire Spottiswoode and Prof. Peter Ryan for helping me with the additional funds during my stay in Cape Town, my almighty God will reward these people.

Thanks to Dr Susie Cunningham, Prof. Peter Ryan, and Hilary Buchanan for your efforts in coordinating the CB course in 2022, just after the pandemic. Thanks to the CB class for the support and encouragement, especially Hal Brindley, Matt Lobenhofer my friend Jenny Jarvis and Cia, and Fran Cox for allowing me to stay in her house with two lovely dogs: my first time to live with dogs inside the house. Finally, thanks my mother and my young brother Abdulkarim and Abubakari for the incredible love, encouragement, and prayers throughout my stays away from home.

Abstract

The greater honeyguide (hereafter "honeyguide") is a wax-eating bird species that engages in a remarkable mutualism with humans. Honeyguides use a specialised chattering call to guide honey-hunters to bees' nests, which honey-hunters harvest with the help of smoke and tools. Honey-hunters increase their harvesting yield by finding bees' nests with the help of honeyguides, and honeyguides feed on leftover beeswax. The relationship between honeyguides and honey-hunters in search of wild bees' nests has been well studied, but we know little about the relationship between honeyguides and beekeepers who harvest honey from man-made beehives. I studied the relationship between people and honeyguides in southern Tanzania, in and/or around Ruaha National Park, Rungwa Game Reserve, and Katavi National Park. I visited 20 villages and interviewed 150 people who either practice beekeeping or honey-hunting or do both. I also visited beekeeping camps to observe how people harvest and process honey, and I set camera traps to investigate the fate of beeswax left behind. Specifically, I asked: (i) what is the relationship between honeyguides and beekeepers? (ii) Does honey-hunting with honeyguides persist in southern Tanzania despite beekeeping and if so, how does it function? (iii) What are the ecosystem effects of honey harvesting in southern Tanzania? (iv) What is the future of human-honeyguide interactions in southern Tanzania? Overall, my results suggest that (i) surprisingly, the relationship between honeyguides and beekeepers is often a mutualism, because beekeepers use honeyguides to find beehives that are ready to harvest, and reward honeyguides with an empty wax comb. (ii) Despite being illegal, honey-hunting with honeyguides persists in southern Tanzania; all 66 honey-hunters mentioned that they use honeyguides to find bees 'nests, and the majority use a specialised calls (particularly "prrrr-prrrr mama") to communicate with honeyguides. (iii) Honey-hunters typically cut down trees to harvest wild beehives, but beekeepers also destroy trees by cutting down or debarking them to make different types of traditional beehives, typically cylinders made of either bark or solid wood. Many beekeepers possess hundreds of hives, suggesting that beekeeping is not less destructive to trees than honey-hunting, and may be more so. (iv) Interview responses suggested that people are losing interest in following honeyguides due to beekeeping replacing honey-hunting, and due to people, who still want to honey-hunt being constrained from doing so by protected areas, and possibly by climate change and habitat loss causing bee declines. Conversely, interview responses also highlighted beekeepers' use of honeyguides to find their own beehives as a reason why human-honeyguide mutualism continues to thrive in southern Tanzania.

1. Introduction

In sub-Saharan Africa, humans and a wax-eating bird species called the greater honeyguide (*Indicator indicator*) interact in a mutualism that benefits both species. There are several species of honeyguide in the family Indicatoridae, but the greater honeyguide (hereafter "honeyguide") is the only species known with certainty to guide people to bees' nests (Cram et al., 2022), which are very difficult for honeyguides to access independently (Isack & Reyer, 1989; Spottiswoode et al., 2016). Honeyguides give chattering calls and fly from one tree to another, to guide the honey-hunter to the bees' nest. In many parts of Africa, honey-hunters use special sounds in return to communicate with honeyguides (Spottiswoode et al., 2016; van der Wal, Gedi, et al., 2022; Wood et al., 2014). After being shown a bees' nest by a honeyguide, honey-hunters then harvest honey from the nest (typically with the help of smoke and tools), and the honeyguide feeds on the leftover bees' wax and bee larvae (Isack & Reyer, 1989; Spottiswoode et al., 2016).

Humans have collected honey for many years now, via both honey-hunting and beekeeping, and honey contributes significantly to the diet of many people (Gruber & Sanda, 2019; Marlowe et al., 2014; Wrangham, 2011). Honeyguides help honey-hunters to increase their harvesting yield (Isack & Reyer, 1989); for example, about 8–10% of Hadza's diet is obtained from honey with the help of honeyguides (Wood et al., 2014). An analogous cooperative relationship between people and wild animals to find food is seen between dolphin species and fishermen in Brazil and Myanmar, in which dolphins herd fish towards fishermen with cast-nets (Zappes et al., 2011). In this case, both species get more fish by cooperating, so this relationship is also a mutualism, which is a relationship that provides a net benefit to both parties (Cram et al., 2022).

Human-honeyguide mutualism is still widespread in Africa, and has been studied in Awer and Boran honey-hunters in Kenya (Isack & Reyer, 1989; van der Wal, Spottiswoode, et al., 2022), in Yao honey-hunters in northern Mozambique (Spottiswoode et al., 2016) and in several cultures in northern Tanzania, particularly Hadzabe people (Laltaika, 2021; Wood et al., 2014). While the mutualism is still thriving in these and other parts of Africa, there have been widespread declines in this relationship in many areas, often because of human restrictions in protected areas, cultural changes meaning people have lost interest in following the birds, and transitions to beekeeping encouraged by development schemes meaning that honey is now increasingly often being obtained from beekeeping rather than honey-hunting of wild bees nesting in natural nest sites (van der Wal, Spottiswoode, et al., 2022).

While the relationship between honeyguides and honey-hunters has been well-studied (Isack & Reyer, 1989; Spottiswoode et al., 2016; Wood et al., 2014), little is known about the nature of the relationship between honeyguide and beekeepers, particularly beekeepers using traditional methods of keeping bees and harvesting honey. We do not yet know whether beekeeping benefits honeyguides (i.e., whether beekeeping provides wax to honeyguides), and whether honeyguides benefit beekeepers (i.e., whether beekeepers stop needing honeyguides, compared to honey-hunters, or whether beekeepers still have a relationship with honeyguides). The main goal of this thesis is to clarify the relationship between honeyguides and traditional beekeepers.

Beekeeping is a form of agriculture that involves collecting honey from bees living in man-made beehives. It is often subdivided into "modern beekeeping” and “traditional beekeeping”. Modern beekeeping produces high-quality honey, typically using top bar hives and Langstroth hives, and in Africa is mostly practiced in South Africa, Kenya, Tunisia, and Egypt (Michael, 2008). Traditional beekeeping is widespread in many African countries and involves different types of hives including bark cylinders, log hives carved from solid wood, woven baskets, and clay hives (Johannsmeier, 2001; Kidd & Schrimpf, 2000). More than 15 types of hives have been identified from western, northern and eastern Africa (Gruber & Sanda, 2019; Hussein, 2000).

Beekeeping has been increasing in Africa, often as part of development initiatives to create opportunities for income in rural areas (Bradbear, 2004; Bradbear et al., 2002; Meilby & Cross, 2019; Nazzi et al., 2014). Beekeeping can bring livelihood and economic benefits to local communities and national economies (Bradbear, 2009; Kandemir, 2003; Schouten, 2020; Shackleton & Pandey, 2014). For example, beekeeping in the Adamaoua savannah and northern montane forests of Cameroon has been reported to contribute 52% of people’s income (Ingram & Njikeu, 2011). Similarly, In Tanzania, more than two million people in rural areas are estimated to be involved in beekeeping (Wawa et al., 2022) In southern Tanzania, honey is obtained from either beekeeping or honey-hunting, and honey is produced by African honeybees (*Apis mellifera scutellata)* or stingless bees (*Hypotrigona* spp.) (Marlowe et al., 2014). Honey is very important in this part of Tanzania (Kashumba, 2018), and all cultural groups here actively interact with wild bees.

Southern Tanzania (my home region) is a particularly interesting area to study the relationship between honeyguides, honey-hunters, and beekeepers because this area is rich in human diversity of cultural groups whose livelihoods range from crop cultivation, livestock keeping, beekeeping, and honey-hunting. However, honey-hunting is thought to be less common here than for example in parts of northern Tanzania (Laltaika, 2021; Wood et al., 2014), and is illegal in protected areas at least in part because of its perceived effect on causing wildfires (Andrew, 2022). The cultural groups of southern Tanzania are closely related and each cultural has different lifestyle and different languages, but also share Kiswahili as the national language.

All cultural groups in these regions are actively engaged in the production of honey and other bee products such as beeswax. Yet, they may differ in type of honey-harvesting process and harvesting method, which might determine their relationship with honeyguides. For example, people can use different methods to harvest honey: some people can use bee suits to harvest honey in beehives, while others can use fires and machete or an axe to harvest honey in bees' nests; this may affect whether and how much wax is left behind. People can also differ with respect to whether they actively reward the honeyguide with empty wax combs. Many honey-hunting cultural groups typically reward honeyguides with empty wax combs after being guided to a bees' nest, as sign of thanks and to motivate the bird to guide them again (Isack & Reyer, 1989; Spottiswoode et al., 2016). Other honey-hunting cultural groups deliberately *don't* reward honeyguides (Laltaika, 2021; van der Wal, Spottiswoode, et al., 2022; Wood et al., 2014). Yet we do not yet know whether beekeepers in southern Tanzania either deliberately or accidentally leave wax available for honeyguides when they harvest beehives.

Variation in honey-harvesting practices also affect their ecosystem consequences. In some parts of Africa, honey-hunters harvest honey by completely cutting down the tree in which a bees' nest is located. Beekeepers also debark trees and cut down trees to construct beehives such as bark cylinder hives and solid wood hives. It is therefore important to document different ways in which people harvest honey. Bees may also face different ecological effects caused by different methods people use to subdue bees. Some honeybee colonies are highly aggressive and attack when first approached by predators such as human honey-hunters, whereas others are less aggressive and only start attacking when people start harvesting (Johnson & Hubbell, 1974). Some beekeepers and honey-hunters use smoke to subdue bees since this reduces the bees' activeness and awareness to defend themselves (Campbell et al., 2018), and sometimes leads to wildfire (Cram et al., 2022). Other people use different methods besides smoke, such as sand or fragrant plants (Kraft & Venkataraman, 2015), which might reduce any negative ecological effects of honey-harvesting.

In this thesis, my aim is to describe and understand the relationship between honeyguides, honey-hunters, and beekeepers in southern Tanzania, and how this may fare in the future. Specifically, I ask four main questions:

1. What is the nature of the relationship between honeyguides and beekeepers?
2. Does honey-hunting with honeyguides persist in southern Tanzania despite beekeeping and if so, how does it function?
3. What are the ecosystem effects of honey harvesting in southern Tanzania?
4. What is the future of human-honeyguide interactions in southern Tanzania?

2. Methods

2.1 Study area

Together with field assistants (Eliupendo Alaitetei Laltaika and Paulo Mkata), we interviewed 150 people from 20 villages belonging to 15 cultural groups. Each of these groups speaks a different traditional language but use Kiswahili as the common language. All villages were in Iringa, Rungwa, Tabora and Katavi Regions, which are all part of southern Tanzania. Each of my study areas was near of one or two protected areas where beekeeping is permitted and takes place: Ruaha National Park, Rungwa Game Reserve, Kizigo Game Reserve, Ugala River and Katavi National Park.

First, I interviewed Hehe, Bena, and Kinga people in Tungamalenga, Kiswila, Ibwanzi, Msembe and Idodi villages in Iringa Region; three of these villages were close to Ruaha National Park. Second, I interviewed Sangu, Nyamwezi, Kimbu, Ngoni, Mwanji, Mlungwa, Mbungu and Gogo people at Mwamagembe, Mitundu, Kambikatoto, Kalagare, Kanoge, Mtendeni, Mgombe, and Kilumbi villages in Rungwa Region; all these villages were close to Rungwa Game Reserve. Third, I interviewed Nyamwezi and Gogo people in Ipole, Katunda, Sikonge, and Kiloleli villages which are all just north of Sikonge town and Sikonge Game Reserve in Tabora Region. Finally, I interviewed Konongo and Sukuma people in Inyonga, Kwamsisi and Kintanula villages in Katavi Region, and these villages are close to Inyonga Game Reserve and Katavi National Park. Sample sizes and a breakdown of cultures per village are shown in Table 1 (indicated in green on Figure 1).

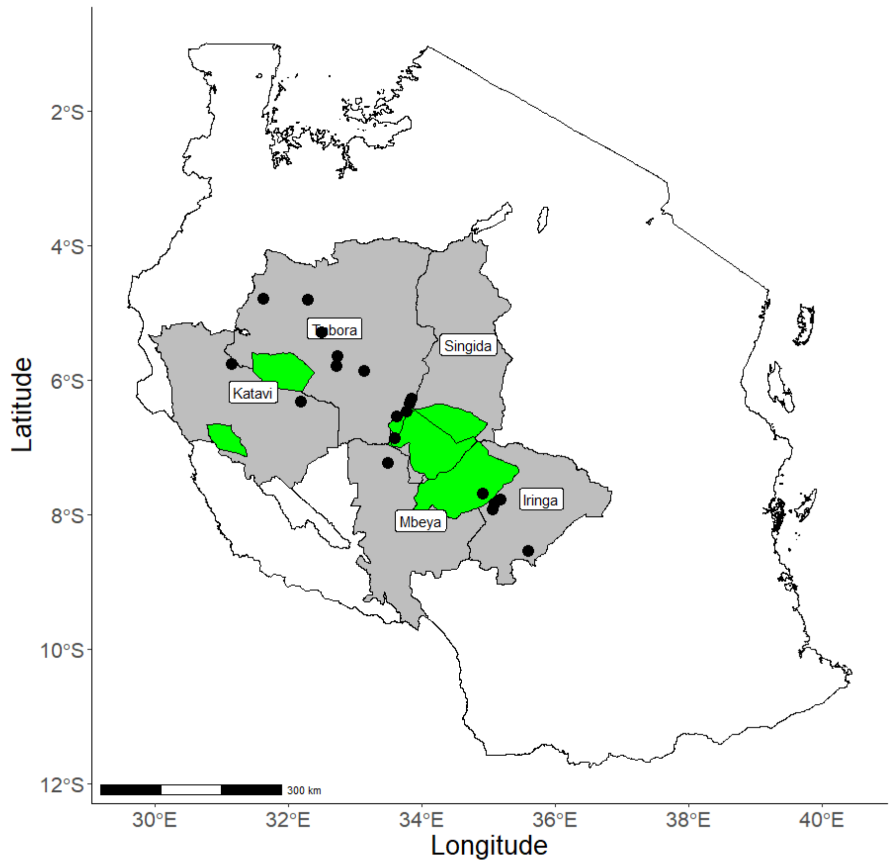


Figure 1 Map showing the four regions and 20 villages surveyed in southern Tanzania; protected areas are indicated in green.

Human cultural diversity in southern Tanzania

First, I worked in Iringa Region, which is close to the Ruaha National Park. Before being gazetted as a National Park in 1964, Ruaha was the part of Rungwa-Ruaha ecosystem and was known as Lunda Game Controlled Area, which consisted also of what is now the Matumizi Bora ya Malihai Idodi na Pawaga (MBOMIPA; meaning “Sustainable Use of Wildlife Resources in Idodi and Pawaga”) and Itigi Thickets Wildlife Management Area (Tarimo & Olotu, 2020). Historically, the Iringa region was dominated by a cultural group known as the Hehe, under chief Mkwawa; they lived in this area before other farming people arrived in Iringa, speaking the Hehe language and Kiswahili (Willoughby, 2012). This cultural group traditionally were farmers and honey-hunters, but nowadays there are many beekeepers. Currently, the Iringa Region comprises several cultural groups, the Hehe, Kinga, Sangu and Bena, whose livelihood ranges from crop cultivation, pastoralism, beekeeping, and honey-hunting. The population in Iringa Region increased by 1,030,349 people in 2020, caused by the high number of migrants

(Dungumaro, 2013; Todd et al., 2017), and also presence of higher learning institutions and expansion of the tourism industry (Mataro et al., 2020).

Second, in Singida region, I worked in the Rungwa area within Manyoni District. The main rainy season is from November–April, and the dry season from June–November (Hariohay et al., 2018; Nahonyo, 2005). This area is close to Rungwa-Kizigo-Muhesi Game Reserve, and is dominated by miombo woodlands which provide habitat for sable antelope (*Hippotragus niger*), African elephant (*Loxodonta africana*), leopard (*Panthera pardus*), Cape buffalo (*Syncerus caffer caffe*r), and spotted hyena (*Crocuta crocuta*) (Hariohay et al., 2018; Nahonyo, 2005). In the Rungwa area there are four main cultural groups: the Kimbu, Nyamwezi, Gogo, and Sukuma. Traditionally people in Rungwa are considered as beekeepers, although part of population also practices honey-hunting.

Third, in Tabora Region, I worked in Sikonge District. This area is dominated by miombo woodlands, and 95% of Sikonge District is covered by forest and game reserves (Kashumba, 2018). The area is known for being the most productive honey production area in Tanzania. In 2020, about 27,000 tons of honey was produced in Tanzania from Tabora Region, and Tabora Region in Tanzania was ranked as the second highest honey producer in Africa (Goerdeler, 2011). The cultural groups who live here are the Nyamwezi, Konongo and Sukuma. Traditionally these people were considered as farmers and livestock keepers, but beekeeping is now a main source of livelihood.

Fourth, in Katavi Region, I worked in Mpanda District, which is located at altitude 1040–1100 m (Silangwa, 2016). This area is dominated by miombo woodland, tropical savanna, grassland and thornbush, and the average mean temperature is 26–30° C (Silangwa, 2016). The main cultural group living here are the Konongo; this is the smallest subgroup of the Sukuma and Nyamwezi people. Traditionally, the Konongo people are agropastoral people who grow crops and keep livestock. However, I also found and interviewed people from the Nyamwezi, Gogo, Kimbu and Ngoni cultural groups here.

In this thesis I refer to the four regions surveyed as Iringa, Rungwa, Tabora and Katavi. Some villages such as Kambikatoto (regarded here as part of Rungwa) are technically in a different administrative region but I pooled them with a very nearby region where I had more samples. Furthermore, Rungwa is technically in Singida Region but here I refer to it specifically as Rungwa because this area has a distinct honey industry.

2.2 Data collection

I carried out fieldwork from September to December 2022, together with Eliupendo Alaitetei Laltaika and Paulo Mkata. Data were collected through (i) interviews, (ii) camera traps and (iii) direct observations in the field, in which we went to observe first-hand how people harvest and process honey on four honey-harvesting trips and eight honey-processing trips. We interviewed 150 people (147 men and 3 women) in 20 villages, spending approximately 40 minutes to one and half hours to interview each participant. The interview questions analyzed are provided in Appendix 1.

Participants were selected with help of the village chairperson, who assisted by identifying individuals who were known beekeepers and/or honey-hunters. First, we read a consent form to each participant (provided in English in Appendix 2) in a commonly understood language (Kiswahili). For those participants who did not understand Kiswahili, we asked a local translator in the village to translate into the local language. We asked each participant to confirm with either their name or their thumb-print that they understood what their answers were going to be used for and were willing to participate. We also asked each participant for permission to audio record their interviews, but some people in each region did not agree for this aspect, for their own reasons. For those that did give permission for audio recording, we used a Tascam DR-05X sound recorder. We made additional notes when participants gave interesting details during interviews. We were careful to avoid participants sharing information to others about the interview content and the answers they gave in reply. To achieve this, we asked our research assistant to ensure that participants selected for interviewed were kept separate from those already interviewed, until the end of interviews. Data collection protocol for this thesis were approved by the University of Cape Town Science Faculty Research Ethics Committee (approval code FSREC 012-2022) and research was carried out under permit from the Tanzania Commission for Science and Technology (permit No. 2022-1018-NA-2022-349).

2.3 Data analysis

I used R 4.2.2 (R Core Team 2022), for all data processing, analyses, and visualizations. In the case of categorical answers to interview questions, I summed the count for each category, per people's occupations (beekeeper, honey-hunter, and people who do both). To test whether the reported litre price of honeybees and stingless bee honey was different between honey-hunters, beekeepers and people who did both, I used linear mixed models (GLM) using the 'lme4 package' (Bates et al., 2015), in which the response variable was the given price per individual, the predictor variable was the occupation, and village as the random factor. Assumptions of normality and homoscedasticity for GLMs were assessed by visual inspection of residuals and normal probability plots. For conversions from Tanzania Shillings (TSh) to US dollars ($), I used the following conversion rate: 1$ = 2230 TSh.

3. Results

3.1 Summary of dataset

All respondents were either beekeepers (n = 84) or honey-hunters (n = 28), or both (n = 38). In Katavi (13 beekeepers, 10 honey-hunters) and Tabora (25 beekeepers, 4 honey-hunters) Regions, respondents were either beekeeper or honey-hunters, whereas in the Rungwa area of Singida Region (15 beekeepers, 37 honey-hunters and 10 were both) and the Iringa Region (31 beekeepers, 4 honey-hunters and 1 was both), some people were both honey-hunters and beekeepers (Figure 2A).

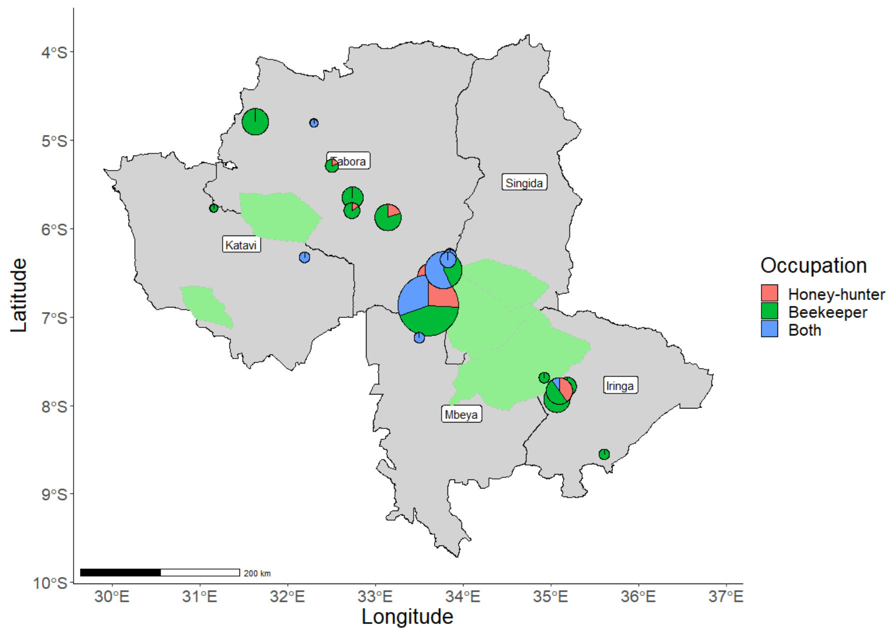
When the 150 respondents were asked about their overall sources of livelihood, 123 mentioned beekeeping (82%), 67 mentioned honey-hunting (45%), 63 mentioned cultivating crops (42%), 21 mentioned animal husbandry (14%), and 3 people (2%) mentioned market activities or another paid job.

In the four regions I surveyed, there were the most cultural groups in Rungwa (9 groups) and Tabora (7), compared to Katavi (4) and Iringa (5) (Table 1; Figure 2B). Different cultural groups are attracted to Rungwa and Tabora Regions because of access to forest resources, and also due to support from the government to do beekeeping. Specially, the Tanzania Forest Service Agency gave land to local communities to support beekeeping. In Katavi there are relatively few cultural groups, probably because the town is not well developed; people here have shifted from livestock keeping to beekeeping. In Iringa, the communities do not have access to forest resources.

Table 1 Overview of number of beekeepers, honey-hunters and people that do both per village, per region. Cultural groups of respondents are indicated per village, and the most commonly represented culture or cultures at each village are indicated in italics.

Region	**Villages**	**Total (n)**	**Beekeepers (n)**	**Honey-hunters (n)**	**People who are both beekeepers & honey-hunters (n)**	**Cultural groups**
Iringa	Tungamalenga	10	5	4	1	*Hehe*, Bena
	Kisilwa	10	10	0	0	Hehe, *Bena*, *Gogo*
	Msembe	4	4	0	0	*Kinga*
	Idodi	7	7	0	0	*Kinga*
	Ibwanzi	4	4	0	0	Bena, *Kinga*
Rungwa	Kalagare	6	0	0	6	Gogo, *Konongo*
	Kanoge	3	0	0	3	*Nyamwezi*
	Kilumbi	4	0	4	0	*Nyamwezi, Kimbu*
	Kambikatoto	4	0	0	4	*Gogo*
	Mgombe	23	10	6	7	*Kimbu*, Konongo, Sukuma, Mlungwa, Nyamwezi
	Mtendeni	5	0	0	5	*Kimbu*, Nyamwezi
	Mitundu	4	0	0	4	Gogo, Konongo, *Sukuma*
	Mwamagembe	14	6	0	8	Kimbu, Mwanji, *Nyamwezi*, Sangu, Hehe, *Konongo*
Tabora	Ipole	6	5	1	0	*Gogo*, Mbugu, Nyamwezi
	Kiloleli	10	8	2	0	*Nyamwezi*, Konongo
	Katunda	5	4	1	0	Ngoni, *Nyamwezi*, Nyiha
	Sikonge	8	8	0	0	Gogo, Mbungwa, *Nyamwezi*
Katavi	Inyonga	3	3	0	0	*Nyamwezi*
	Kwamsisi	10	10	0	0	Nyamwezi, *Konongo*
	Kintanula	10	0	10	0	Nyamwezi, Ngoni, *Gogo*, Kimbu
Total	**20 villages**	**150**	**84**	**28**	**38**	

(A)



(B)

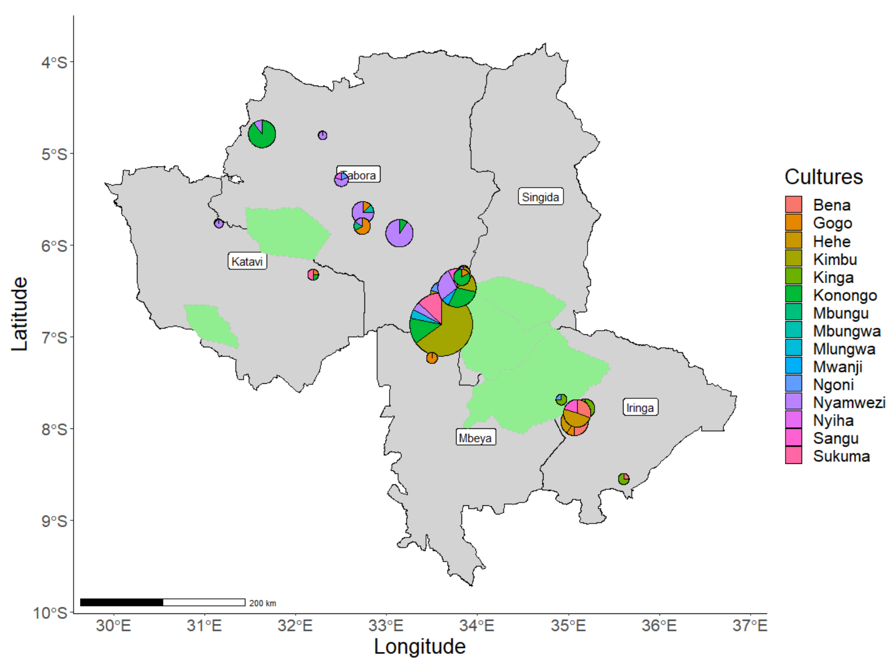


Figure 2 (A) Peoples' occupations (honey-hunter, beekeeper, or both) and (B) cultural groups across interview locations. The size of the pie charts is proportional to the sample size of interviews per village.

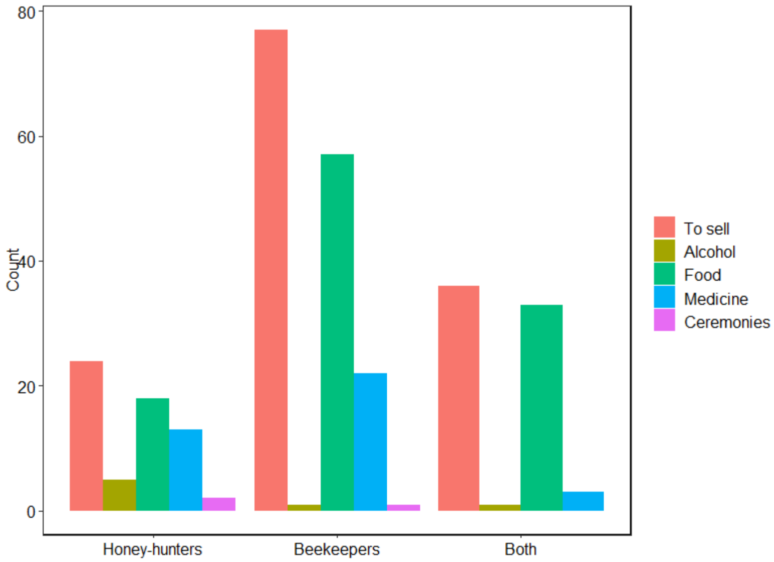
3.2 Uses and value of bee products in southern Tanzania.

Honey uses

All respondents reported using honeybee honey. When asked what they used honeybee honey for, the majority said food (72%) and to sell (91%), but some also used honey as medicine (25%), to brew alcohol (5%), and in ceremonies (particularly traditional weddings) (3%). Figure 3A shows that honeybee honey was used for similar purposes by beekeepers, honey-hunters and people who do both. Fifty-four out of 66 honey-hunters (82%) mentioned that selling honey is their main source of income in the honey-hunting high season, and 121 out of 122 beekeepers (99%) mentioned that the main reason motivating them to keep bees is to collect honey to sell.

Stingless bee honey was also widely used. Overall, 129 of the 149 respondents (87%) mentioned that they used stingless bee honey. This was mostly for medicine (61%; e.g. to treat ulcers) and food (53%), but also sold (18%), and to make alcohol (1%) and in ceremonies (1%). Like for honeybee honey, stingless bee honey was used for similar purposes by beekeepers, honey-hunters and people who do both (Figure 3B).

(A)



(B)

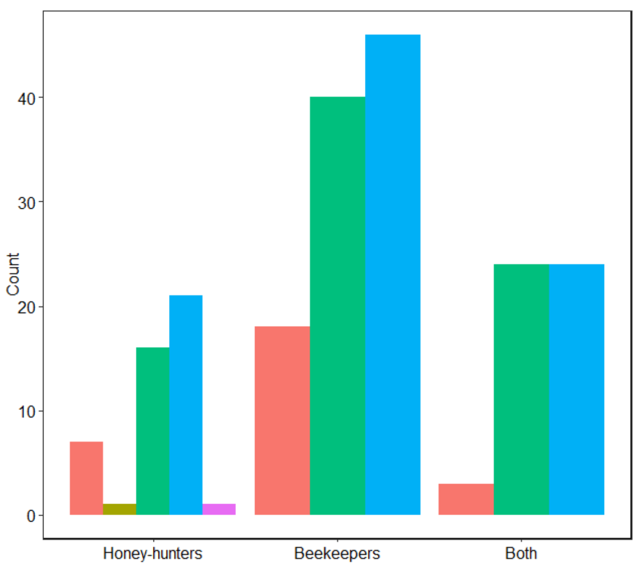


Figure 3 Variation in honey use across beekeepers, honey-hunters, and people who do both for (A) honeybee honey (n = 149) and (B) stingless bee honey (n = 131). Some people gave multiple answers, so the bars do not sum to 100%.

We asked respondents what to the best of their knowledge the current market price of honey was. Many respondents provided a price per 20 litre container of honeybee honey rather than per 1 litre of honeybee honey, as that is a more common unit. For honeybee honey (n = 150 respondents), the mean ± SE reported price per litre for honeybee honey was 4095 ± 68 SE Tsh (range 2,500–7,500 Tsh, or

US$ 1–3). Beekeepers, honey-hunters, and people who do both did not significantly differ in the reported average litre price of honeybee honey (GLM, all $p > 0.05$; Figure 4A). For stingless bee honey (n = 122 respondents), the mean ± SE reported price per litre was 14,443 ± 261 TSh (range: 7,000–20,000 Tsh, or US$ 3–9). Beekeepers, honey-hunters and people who do both did not significantly differ in the reported average litre price of stingless bee honey (GLM, all $p > 0.05$; Figure 4B).

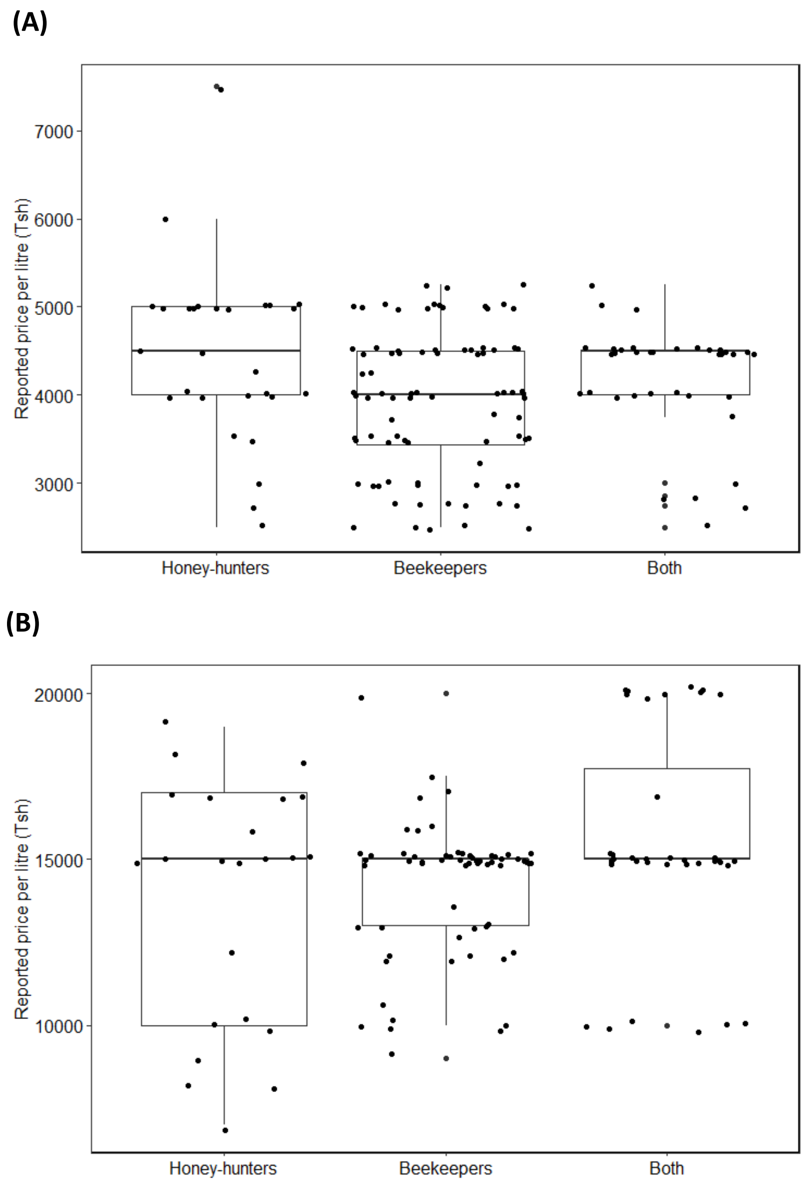


Figure 4 Reported prices of honey per litre for (A) honeybee honey (n = 150 respondents) and (B) stingless bee honey (n = 122 respondents).

Beeswax use

Beeswax was also widely collected by both honey-hunters and beekeepers. Twenty-eight honey-hunters (19%), 84 beekeepers (56%), and 38 people who do both (25%) mentioned that they used beeswax to make purified blocks of wax and sold these to the external market. I did not collect quantitative data on responses for the uses of wax, but some people mentioned that the wax sold is ultimately used to make soap, candles, and as layering on plastic shoes. There is a strong market for wax, because of good infrastructure to transport wax to the external market. Blocks of wax are prepared from empty wax combs left over after the honey is squeezed out of them, and from empty wax combs found in the bees' nests. Informal conversions with some respondents (n = 5) revealed that wax is sold at a higher value per kg than honey, on average 30,000 Tsh (US$ 13).

3.3 Seasonality of honey flow

Honey flow in southern Tanzania varies from region to region; this is highly dependent on the rainfall pattern per region. During the rainy season, more trees produce flowers and so people expect more honey. Mostly, honey flow is said to be best in June, July, August, and up to early September, but this varies a little between regions (Figure 5).

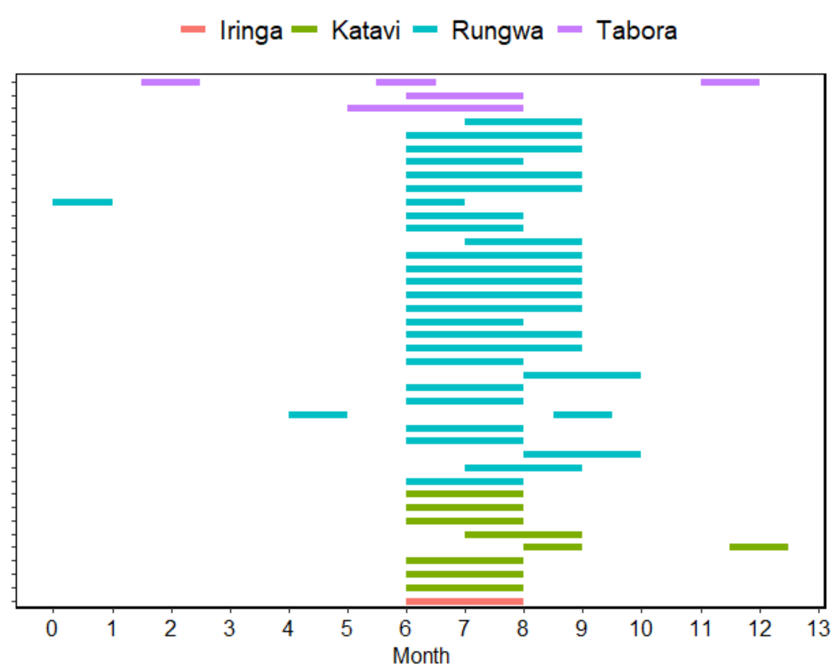


Figure 5 The best months for honey-hunting according to honey-hunters (n = 45), per region.

3.4 Beekeeping practices and culture

Hive types

Three different types of beehives are used (Figure 6). First, the bark cylinder hive (used by 63% of beekeepers) is made from the bark of a tree (harvested locally from indigenous trees), forming a natural cylinder. This hive type is popular because it is reliable and less expensive compared to other types of hives (especially compared to a box hive), but is not very durable so only remains in use for about two years. Second, the solid wood hive (used by 80% of beekeepers) is made using solid wood (also locally harvested from trees using chainsaws) and nails. This hive type is strong and can remain in use for 2–5 years, in contrast to a bark cylinder hive that disintegrates much quicker. Third, the box hive (used by 40 [34%] of beekeepers) is made of commercial timber, lined on the outside by metal or tin material. This hive type is mostly used by high-income beekeepers, given its high price of up to 350,000 Tsh (US$ 157) per hive.

(A) **(B)**

Figure 6 Different types of traditional beehives used in southern Tanzania. (A) Bark cylinder hive. (B) Solid wood hive under construction.

Beekeeping camps

Beekeepers honey-harvest in groups, and many of they stay in beekeeping camps to facilitate larger-scale honey-harvesting. Twenty beekeepers (16%) interviewed were in beekeeping camps at the time of the interview. Beekeeping camps are places where a group of beekeepers stays for up to four months at a time, to install beehives and later harvest and process honey. Beekeeping camps are active twice a year: once to construct and prepare the hives and hang them in trees, and a second time to check and then harvest the hives that are filled with honey. In the two beekeeping camps we visited, we found that the camps were divided into two main areas, where beekeepers respectively harvest the honey from beehives, and process the honey. People sleep in beds made from tree branches, and have a storeroom for food, water and other equipment used for honey harvesting and honey processing.

Honey-harvesting by beekeepers

When beekeepers harvest honey, they often use a bee suit (mentioned by 22% of beekeeper respondents), a smoker (mentioned by 81% of beekeeper respondents) and carry large wooden spoons to remove wax combs filled with honey from the hives. At the two beekeeping camps I personally observed, the wax combs with honey are placed in a pile and the honey squeezed out into a plastic bucket, either using a car jack or a brick firing machine when a car jack is not available. Then, honey is transferred to an oil drum or other container and is ready to be sold. (Figure 7).

Wax block and "honey water" production by beekeepers

At the two beekeeping camps I personally observed, blocks of wax (Figure 7D) are prepared from empty wax combs left over after the honey is squeezed out of them, and from empty wax combs found in wild bees' nests (Figure 7A). After the honey has been extracted, the beekeepers then took the leftover wax and boiled it in hot water in a big container (Figure 7B), and then filtered this to get a sweet water which is added to local beer to provide flavour and a sweet smell. After the honey water is filtered out, the dirty leftover material (comprised of e.g., the fibrous casings of old hatched bee larvae and other residue), called "manure wax" (Figure 7C), is dumped on the ground at the edges of the camp.

Reasons for not honey-hunting

When beekeepers were asked why they don't collect honey from wild bees, 112 people (92%) mentioned it is easier to keep bees, 28 people (22%) mentioned restricted access to protected areas, and 5 people (4%) mentioned that there were not enough wild bees in the area.

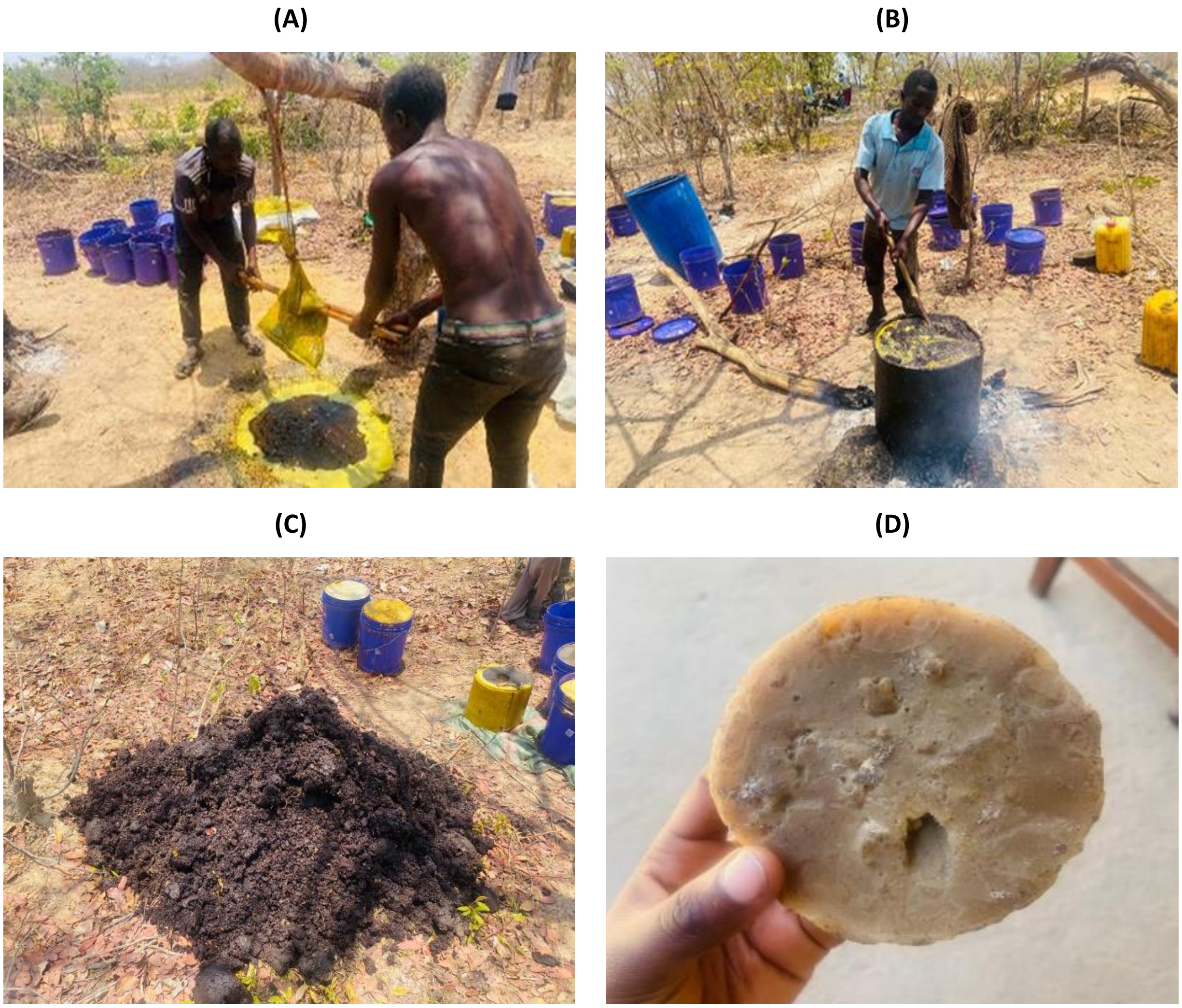


Figure 7 People in a beekeeping camp producing a pile of wax from empty wax combs. (A) Two beekeepers squeezing the honey water from empty wax combs. (B) Beekeeper boiling empty wax with hot water to make solid wax. (C) "Manure wax", after squeezing out the honey water. (D) Final purified wax product.

Economic value of beekeeping

The number and size of harvests per beekeeper depends on the type and number of hives used. From informal conversation with some respondents, we learnt that one solid wood or box hive can produce 40 litres of honey, whereas one bark cylinder hive can produce 20 litre of honey. Out of 122 people that kept bees, 77 said they used bark cylinder hives, 97 said they used solid wood hives and 39 said they used box hives. Seventy-two respondents used multiple hive types. Respondents reported that a bark cylinder hive costs 7,000 Tsh (ca. US$ 3), a solid wood cylinder hive costs 200,000 Tsh (ca. US$ 90) and a box hive costs 350,000 Tsh (ca. US$ 157). Of the people that mentioned that they had at least one of that hive type, the people had a mean ± SE of 96 ± 11 bark cylinder hives (range: 1–600), 176 ± 14 (range: 7–643) for solid wood hives, and 117 ± 16 (range: 5–380) for box hives (Figure 8). In total, the 122 beekeepers together reported owning 7,411 bark cylinder hives, 17,172 solid wood hives, and 4,571 box hives. Despite being expensive, solid wood hives are widely used by the beekeepers, since they have advised by the government that by 2025 every beekeeper should be using solid wood hives rather than bark cylinder hives.

To get a rough idea what the profit margin is for a beekeeper, we can look at the example of bark cylinders only. If we take the average number a bark cylinders per person (96) and multiply that with the maximum amount of honey that is reportedly gained from these hives (20 litres), and assume (based on conversations with beekeepers) that 60% of hives are occupied by bees and harvestable in a given season, a single beekeeper can produce 96 * 20 * 0.6 = 1,152 litres of honey in a single season. Given that one litre of honey is sold for on average 4,095 (generating 960 X 4,095 Tsh = 4,717,440 Tsh or US$ 2115), minus the costs of 96 bark cylinder hives (96 x 7,000 TSh = 672,000 TSh or US$ 301), a beekeeper with an average number of hives can make a profit of approximately 4,045,440 Tsh (US$ 1,814) in a season from bark cylinder hives alone. This does not include other costs not measured like transportation costs. Note that this rough estimate also not consider the other hive types that a beekeeper can have. The hives themselves also contribute to the local economy, via the carpenter and other people involved in hive construction.

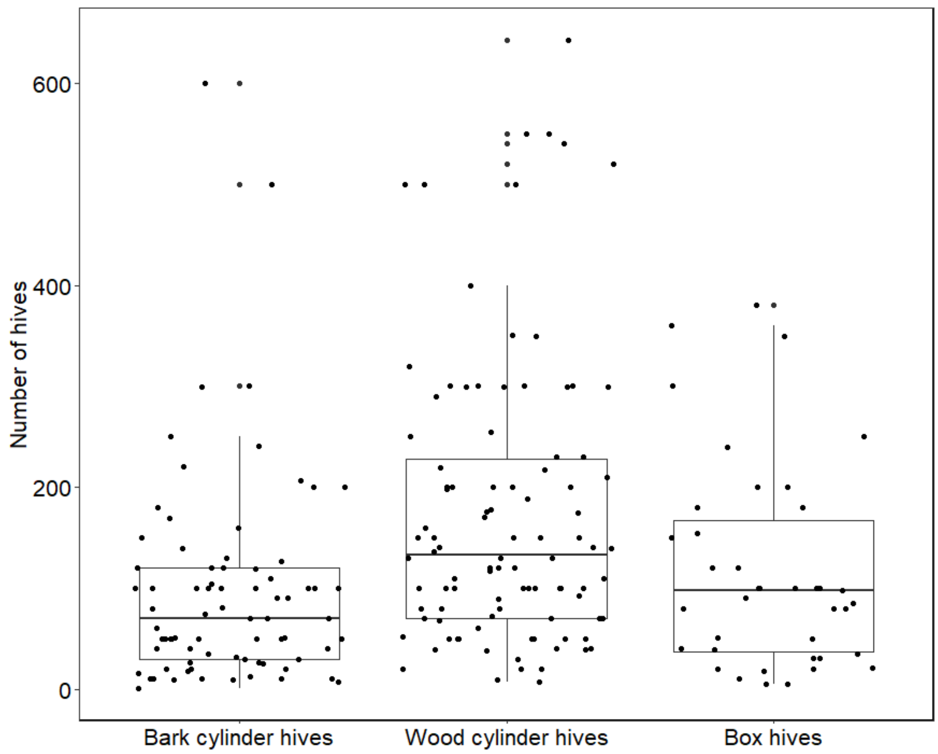


Figure 8 Number of beehives owned by respondents, per hive type (n = 122 beekeepers).

Beekeeping localities

All respondents mentioned that they hang their hives in natural forests (which in the area is typically miombo woodland), except beekeepers in Iringa (n = 31) where people keep bees on or near their farmlands. Many beekeeper respondents from Rungwa (76%) Tabora (43%), and Katavi (19%) mentioned that they were given forest land by the government to support beekeeping projects, and they are legally registered by the Tanzania Forest Agency as the qualified beekeepers. Many beekeeping projects in Rungwa, Tabora and Katavi are supported and encouraged by NGOs. This is not common in Iringa, where people are not given forest land for beekeeping and so keep bees outside their houses and their own farmland plantation.

3.5 What is the relationship between honeyguides and beekeepers?

Do beekeepers benefit from honeyguides?

Across the four regions we surveyed, I found that beekeepers benefit from honeyguides. Thirty-two beekeepers mentioned incidentally that they follow honeyguides to find those among their beehives which are ready to harvest. These same thirty-two beekeepers reported using whistles to attract a honeyguide and/or sing traditional song while following it, just as honey-hunters do (see next section).

Furthermore, ten beekeepers incidentally reported that honeyguides can also be used as a cue by beekeepers; when a honeyguide is present at a hive, the beekeepers see this as a sign that the hive is occupied by bees, and therefore likely ready to harvest. So even though beekeepers typically know the locations of their hives, signals or cues from honeyguides are still useful to them because they have hundreds of hives and not all are occupied by bees.

Do honeyguides benefit from beekeepers?

I found that honeyguides are also benefiting from beekeepers. I asked beekeepers what they do with empty wax combs, to see if wax from beekeeping might become available for honeyguides. Approximately a third of people keeping bees mentioned leaving empty wax combs and squeezed out wax combs out specifically for honeyguides (Table 2). These results indicate that honeyguides also benefit from beekeepers.

Table 2 Responses of people who keep bees (n = 122; pooling both specialist beekeepers and people who practice both beekeeping and honey-hunting) on what they do with different components of the contents of the beehive. Note some people gave multiple answers, so the answers do not always sum to 100%.

	Taken home	**Left in hive**	**Left for the bird**
Wax combs with honey	100%		
Wax combs with brood	2%	98%	
Empty wax combs	37%	27%	36%
Squeezed out wax combs	92%		29%

Given that our findings show that beekeepers and honeyguides mutually benefit from one another, we can describe the relationship between honeyguides and beekeepers as at least largely mutualistic.

3.6 Honey-hunting practices and cultures

Current state of honey-hunting with honeyguides

Despite the popularity of beekeeping, honey-hunting of wild bees persists in southern Tanzania. Of the 150 people I interviewed, 66 people reported that they practice honey-hunting; and of these 28 were specialist honey-hunters and 38 were people who practice both honey-hunting and beekeeping. The majority of honey-hunters (62 out of 70; 88%) reported that they go into the forest specifically for honey-hunting trips, while 8 out of 70 (11%) reported that they only honey-hunt opportunistically while busy with other activities like herding cattle.

Of these 66 people who honey-hunt (including those that do both), 60 (88%) were still active honey-hunters, defined as people who have honey-hunted in the last year. All the honey-hunters we interviewed (n = 66) said that they use honeyguides to find wild bees: 88% said they most often use honeyguides, 6% said they sometimes do, and 6% said they always do (Figure 9). Interestingly, 39 out of 66 honey-hunters (59%) said they use honeyguides to find stingless bees' nests.

Of these 66 honey-hunters, 94% reported that they reward honeyguides with empty wax combs after being guided to bees' nests, while nobody reported rewarding honeyguides when guided to the stingless bees' nests. Seven honey-hunters explained why they do not reward stingless bees': six honey-hunters mentioned that there is too little wax comb and honey in stingless bees' nests, so they can't reward honeyguides, and one honey-hunter mentioned that stingless bees have a very soft comb that is easy to destroy when honey-harvesting, so nothing is left for honeyguides.

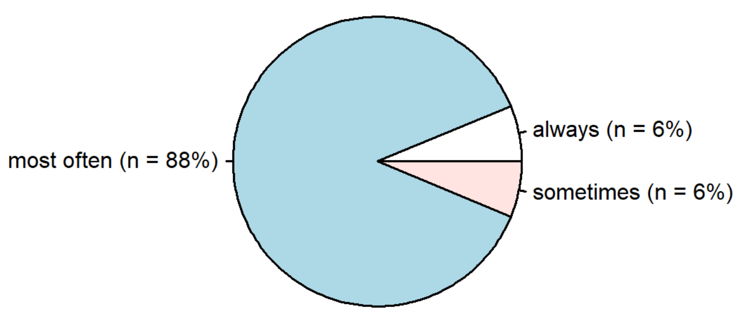


Figure 9 The frequency with which honey-hunters (n = 66) reported that they use honeyguides to find wild bees' nests.

Methods used to attract and follow honeyguides

Fifty-four out of 66 honey-hunters mentioned that use sound to communicate with honeyguides. I asked honey-hunters to specify what type of sound they used to communicated with honeyguides, in two different phases: to attract the bird ("recruitment call"), and to communicate with the bird after it has arrived ("coordination call"). To recruit honeyguides, 19 out of 47 honey-hunters (40%) said they used a specific recruitment call ("prrrr-prrrrr mama") to attract honeyguides, while 11 honey-hunters (23%) said they simply used whistles to attract honeyguide, 9 honey-hunters (19%) said they used a specific recruitment call "rrr rrr" to attract honeyguides, 3 honey-hunters (10%) said simply chop trees to make sound, 3 honey-hunters (6%) said they sing "ligaliga mama" to attract honeyguides, and 2 honey-hunters (4%) said they sing traditional songs that express love to honeyguides. As coordination calls, 16 honey-hunters (34%) said they used "rrr rrr'' sound, 10 honey-hunter (23%) said they used whistles, 6 honey-hunters (14%) said they used a "pre pre" sound and 3 honey-hunters (6%) said they used "ligaliga mama", and 5 honey-hunters (11%) used traditional songs in which honeyguides are praised as "mama". "Ligaliga mama" is used as an emotional plea to honeyguides to show them honey; some people are said to cry when using these words.

Honey-hunters also reported that they have modified their use of sound to communicate with honeyguides, since they are afraid to be caught by the park rangers: four honey-hunters and two people who both honey-hunt and keep bees mentioned that have stopped using a call to communicate with honeyguide and rather hit trees to attract honeyguides, and then follow honeyguides silently until they find honey.

Honey-harvesting by honey-hunters

Honey-hunters normally go out honey-hunting in groups: 95% of honey-hunters reported that they always go with others, and 5% reported they go always or mostly alone. Honey-hunters normally carry a backpack, an axe, machete, bucket, rope, and match box. Twenty-eight (42%) of honey-hunter respondents incidentally mentioned that they cut down the trees when harvesting honey (they were not systematically asked whether they cut down trees). When honey-hunters harvest honey from a bees' nests, they first make efforts to subdue the bees. Honey-hunters do not use bee suits or smokers like beekeepers generally do. Instead, they often using smoke from a fire (65 of 66 honey-hunters reported this). One respondent mentioned grinding cassava leaves and pouring this powder into the bees' nest to subdue the bees. Next, one person is in charge of harvesting the bees' nest, either by cutting out a hole around the best, or by cutting down the tree. Once the bees' nest is accessible, a second honey-hunter will join to take out the wax combs with honey, using a machete. Close to the bees' nest, honey is squeezed from the wax combs into the bucket using two hands.

Most honey-hunting activity is carried out in the same forests where people also keep bees, which are typically protected areas where beekeeping is permitted but honey-hunting is illegal. Thirty-eight respondents out of 66 people who honey-hunt (i.e. both honey-hunters and people who both keep bees and honey-hunt) (58%) incidentally mentioned that some honey-hunters take advantage of beekeeping so that they can have access to honey-hunting in the forest.

3.6 The ecosystem effects of honey-harvesting

Tree cutting

Honey-hunters show ownership of bees' nests, and put a mark on the tree when they find a wild bees' nest but want to harvest it at a later date, to protect it from other peoples' harvesting the honey. Some honey-hunters (42%) incidentally mentioned that they try to avoid chopping down of trees when harvesting honey.

Given that beekeepers use many different hives per person, beekeeping also has significant effects on trees (Figure 10). Many respondents reported they used bark cylinder and solid wood hives which are made from local trees. From informal conversation I learnt that four bark cylinder and four solid wood hives can typically be made from a single tree. Given that people own on average of 176 solid wood hives (and 96 bark cylinder hives), that need to be replaced every 3.5 years (range: 2–5 years as indicated above), this suggests that a beekeeper on average needs about 176 / 4 / 3.5 = 13 trees per year. These results suggest that although honey-hunters affect the environment by sometimes cutting down trees, beekeepers possibly have a similar or possible even bigger effect on the environment given the scale at which beehives are produced.

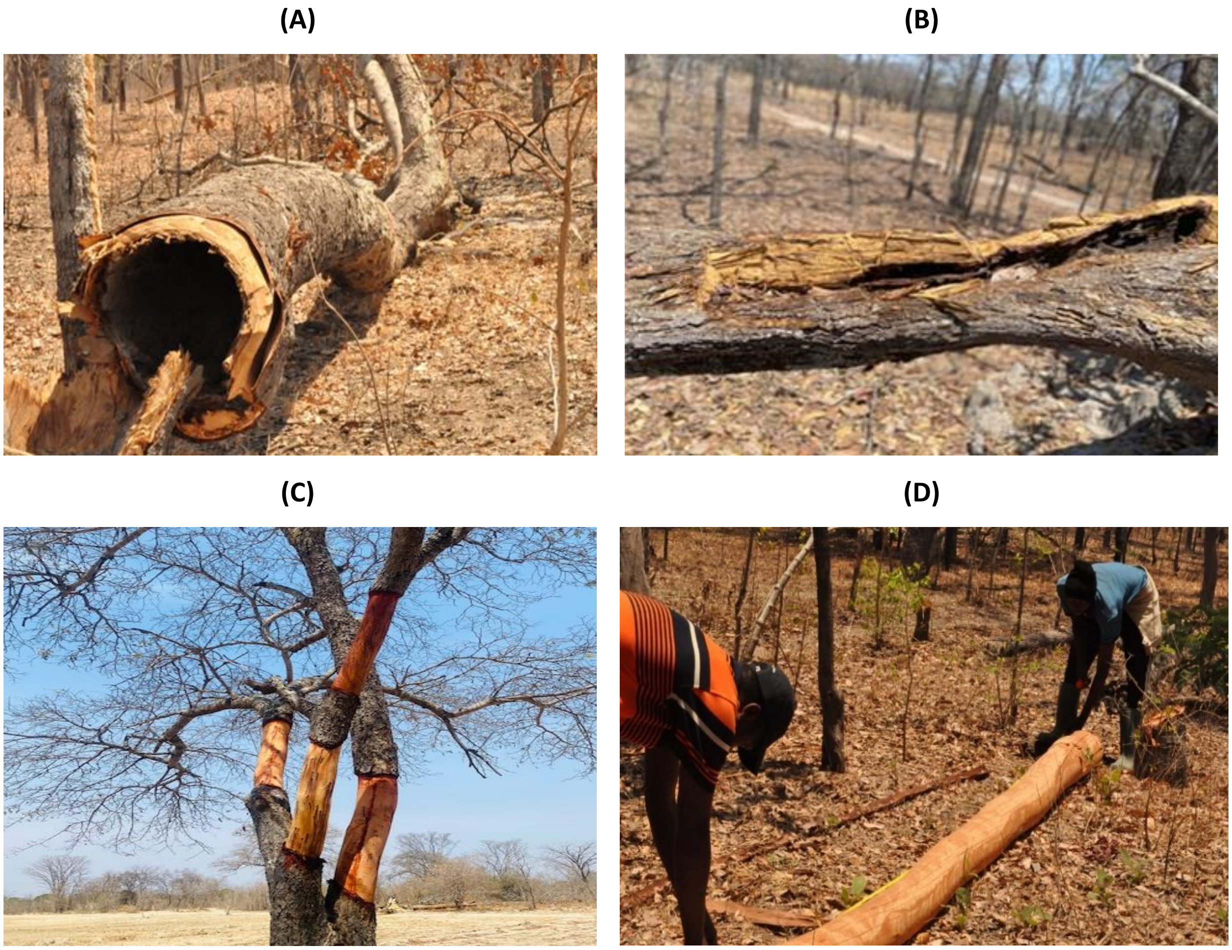


Figure 10 Ecosystem effect on trees. (A) Tree cut by beekeepers to make solid wood hives. (B) Tree cut down for harvesting by honey-hunters. (C) Tree debarking by beekeepers to made bark cylinder hives. (D) Dead tree after debarking.

Use of fire and smoke

Honey-hunters typically use smoke from an open fire to subdue bees (65 of 66 honey-hunters; 98%) compared to the beekeepers who rather use a bee suit and/or a smoker (108 of 116 beekeepers; 93%).

Wax availability to other animals

Honey-harvesting also affects other animals in the ecosystem (besides honeyguides) that eat wax. Camera traps (Acorn 6210; Ltl Acorn, Denmark, Wisconsin) we set in beekeeping camps showed that several other species also benefit from beeswax. A genet *Genetta* sp. was seen visiting a wax pile twice, in both day and night, and was seen to eat wax (Figure 11A). Babblers (*Turdoides* sp.) were seen three times visiting a pile of manure wax, and a glossy starling (*Lamprotornis* sp.) was seen once visiting a pile manure wax; it is likely that these species were eating invertebrates feeding on the manure wax. An elephant (*Loxodonta africana)* was seen visiting a pile of wax manure at night but was not observed to eat anything (Figure 11B). I asked respondents what other animals besides honeyguides they thought eat wax, and they mentioned baboons (26 out of 84; 31% of respondents), mongooses (Herpestidae) (22 out of 84; 26%), honey badgers (*Mellivora capensis)* (4 out of 84; 17%), bush pigs (*Potamochoeerus larvatus)* (8 out of 84; 10%), serval cats (*Leptailurus serval)* (14 out of 84; 17%), genets (*Genetta* sp*.)* (8 out of 84; 10%), elephants *(Loxodonta africana*) (3 out of 84; 4%), bush rats (species unknown) (1 out of 84; 1%), civet (1 out of 84; 1%), 1 rock hyrax (*Procavia capensis*) (1 out of 84; 1%) and wild dogs *(Lycaon pictus*) (1 out of 84; 1%) (Figure 12).

(A) **(B)**

Figure 11 Camera trap images at wax. (A) Genet (*Genetta* sp.); (B) elephant (*Loxodonta africana*).

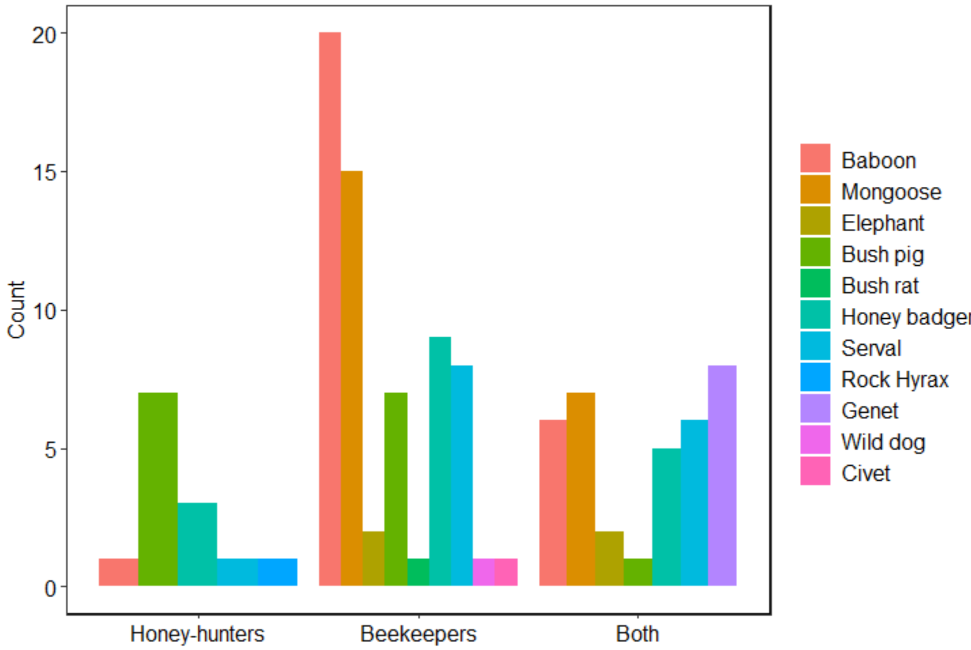


Figure 12 Animal species other than honeyguides that respondents stated eat wax left behind by honey-hunters and beekeepers.

3.7 What is the future of honeyguide-human interactions in southern Tanzania?

Ages of honey-hunters and beekeepers

Some cultural groups were seemed to be purely honey-hunters, whereas others do both honey-hunters and beekeepers. In Rungwa, some cultural groups are active honey-hunters (Nyamwezi, Kimbu), whereas others are beekeepers (Nyamwezi, Konongo). Similarly, in Tabora and Katavi, some groups are active honey-hunters (Ngoni, Nyamwezi, Mbungwa, Nyiha, Mbugu, Gogo, Konongo) and other are beekeepers (Nyamwezi, Gogo, Mbungwa, Nyiha, Ngoni, Mbugu, Konongo). In Iringa, some groups (Hehe, Bena, Kinga) are active honey-hunters and others are mostly beekeepers (Hehe, Bena, Kinga, Sangu, Gogo, Ngoni). In all four regions, the ages of beekeepers and honey-hunters showed a very similar distribution (Figure 13).

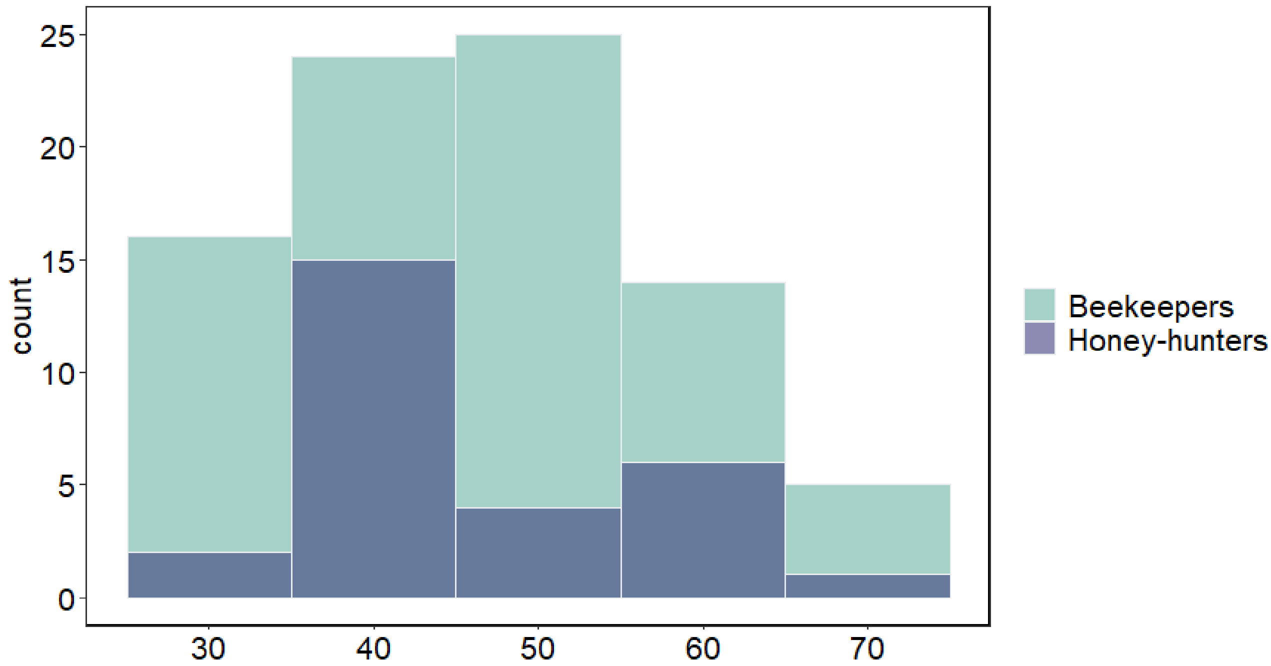


Figure 13 Histograms showing the age distributions of beekeepers (n = 84) vs honey-hunters (n = 28).

Cultural transmission of skills

Respondents reported that they had learnt honey-hunt from family members or friends. Sixty of 66 honey-hunters (91%) reported that they learnt to honey-hunt from their fathers, fourteen (21%) from their friends, two (3%) from their grandfathers, and one (2%) from a peer. Fourty-eight of 66 honey-hunters (73%) said that they learnt to honey-hunt in the same place they currently live and where I interviewed them.

Peoples' perception of changes in human-honeyguide interactions in the future

To understand whether the honeyguide-human interaction is changing over time, I directly asked whether people thought the interaction will exist in the future. Overall, among all respondents (n = 150), 50% of people replied that the interaction will exist; 48% of people replied that it will not exist, and one was unsure. The main reasons given for a *decrease* in human-honeyguide interactions were, first, people losing of interest because of education and changed livelihoods (reported by 27% of honey-hunters and 12% of beekeepers); second, habitat loss and climate change (24% of honey-hunters and 15% of beekeepers); third, beekeeping replacing honey-hunting (13% of honey-hunters and 21% of beekeepers); and fourth, restricted access to protected areas, given that honey-hunting is illegal in protected areas in Tanzania (14% of honey-hunters and 15% of beekeepers). The main reasons given for an *increase* in human-honeyguide interactions were, first, that honey-hunters are still interacting with honeyguides (9% of honey-hunters and 8% of beekeepers) and second, that beekeepers are also interacting with honeyguides to find beehives which are ready to harvest (9% of honey-hunters and 23% of beekeepers) (Figure 14).

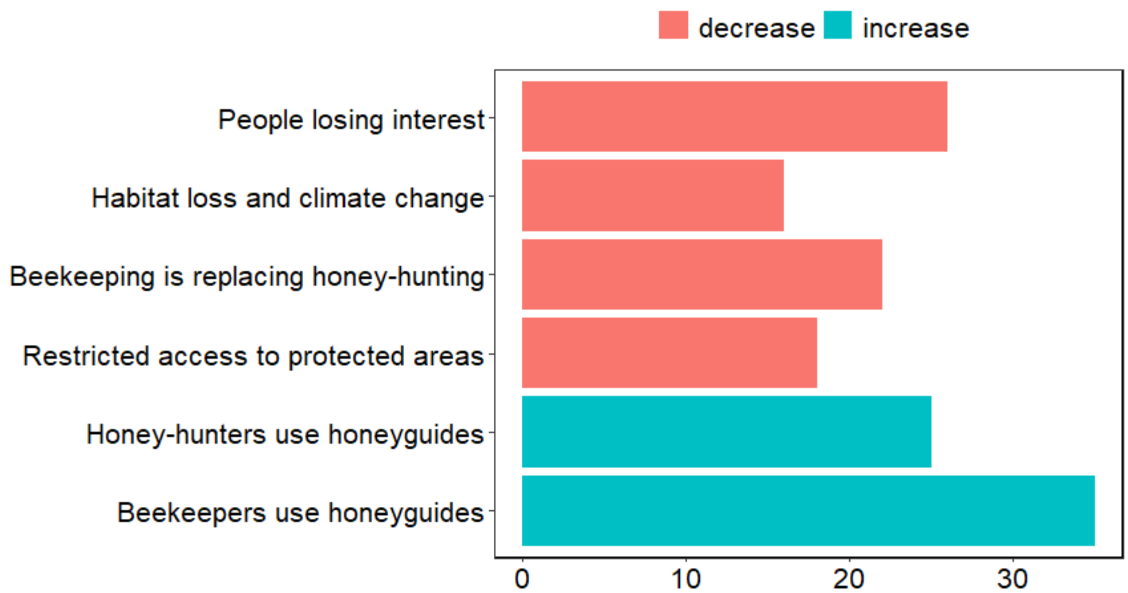


Figure 14 Respondents' perceptions of reasons for changes in human-honeyguide interactions (n = 66 honey-hunters and 84 beekeepers).

I also asked honey-hunters in particular (n = 66) whether specifically the role of honeyguides in honey-hunting had changed over time; 48 out of 66 honey-hunters (73%) replied that there had been no change and 18 out of 66 honey-hunters (27%) replied that it has changed. The reasons given for a *decrease* in the role of honeyguides in honey-hunting over time were, first, that people are not using sound anymore to communicate with honeyguides to hide from park rangers (reported by 6 out of 25 honey-hunters 24%). Second, that people have lost interest in following honeyguides (reported by 7 out of 25 honey-hunters; 28%). Reasons given for an *increase* in the role of honeyguides in honey-hunting were that people are still cooperating with honeyguides to find the bees' nests in a similar way to when respondents were young (reported by 8 out of 25 honey-hunters; 32%), and that beekeepers are now cooperating with honeyguides to find occupied beehives (reported by 4 out of 25 honey-hunters; 16%) (Figure 15).

Threats to honey-hunting

Honey-hunters in southern Tanzania are regarded as poachers of forest resources, and so their honey-hunting practice is facing threats. Forty-eight people of 66 honey-hunters (73%) replied that honey-hunting practices had changed since they were young. The main reasons given for these changes were, first, restricted access to protected areas, since honey-hunting is regarded as poaching (4 out of 48) honey-hunters; 8%). Second, that beekeeping is replacing honey-hunting since beekeeping projects are encouraged by the government and NGOs (33 out of 48 honey-hunters; 69%). Third, that honey-hunting culture is being lost (34 out of 48 honey-hunters; (71%). Informal conversations with some respondents suggested that the existence of both honey-hunting and beekeeping in the same place could threaten honey-hunting practices, since people might be influenced to take up beekeeping.

4. Discussion

I investigated the relationships between honeyguides, honey-hunters, and beekeepers in southern Tanzania. To do so I interviewed 150 people in 20 villages in four regions (Iringa, Rungwa, Tabora and Katavi), and specifically asked questions relating to the use and value of bee products, the methods used to harvest honey, the relationship between honeyguides and beekeepers, the relationship between honeyguides and honey-hunters, the ecosystem effect of honey-harvesting, and the likely future of human-honeyguides interactions this region.

Bee products are a big industry in southern Tanzania. I found that honeybee honey, stingless bee honey, and honeybee wax are all important bee products. Both types of honey are used to sell, to brew alcohol, as food, as medicine, and in ceremonies. Honeybee wax is purified and sold for the local market as well as for export to neighboring countries. Many respondents across all four regions commented that the market demand for honey from other East African countries is so high that many people are active in both beekeeping and honey-hunting of wild bees' nests, to try to meet this demand.

Beekeeping is therefore carried out at a large scale in southern Tanzania. Some beekeeping projects have been encouraged by development schemes and the government, and many people are engaged in these activities. In the Rungwa, Katavi and Tabora regions, most beekeepers (and people who both honey-hunt and keep bees) told me that the government has provided forest resources to do beekeeping, and that NGOs are supporting this by providing beehives such as box hives, and by helping to reach honey markets outside the area. In the Iringa region, like in northern Tanzania (Laltaika, 2021), this is less common, and Hehe beekeepers in Iringa and Maasai beekeepers in northern Tanzania are not supported by government and rather decide to keep bees in their farmland.

What is the nature of the relationship between honeyguides and beekeepers?

The mutualistic relationship between honey-hunters and honeyguides has been well-studied (Isack & Reyer, 1989; Spottiswoode et al., 2016; Wood et al., 2014); in this thesis, I first I investigated the relationship between honeyguides and *beekeepers*, which is not well understood. For example, we could expect that both beekeepers might benefit honeyguides via waste wax but receive no benefit themselves, since beekeepers shouldn't need honeyguides to find their own hives. This would be a form of commensalism (Mathis & Bronstein, 2020).

Instead I found that interestingly, beekeepers do actively cooperate with honeyguides, specifically to find which hives are ready to harvest. Even though beekeepers know where their hives are, honeyguides are still useful to them because they have hundreds of hives and not all are occupied by bees. Beekeepers also reward honeyguides, by leaving empty beeswax and wax leftovers after squeezing out the honey, and they do so specifically for honeyguides to eat. Beekeepers also use the presence of honeyguides perched near their hives (but not specifically guiding them) as a cue that a hive is ready to harvest. Whether beekeepers are actively guided to occupied hives by honeyguides, or use honeyguides has a passive cue that hives are ready to harvest, in both cases beekeepers benefit from honeyguides. Since people typically specifically leave wax for honeyguides, honeyguides benefit from beekeepers too. These interactions were consistent across the four regions I studied, even when these regions were geographically far from one another. The relationship between honeyguides and beekeepers is therefore often a mutualism (Table 2).

Based on my findings in southern Tanzania, I speculate that there could even be a three-way mutualism between honeyguides, beekeepers, and honey-hunters. First, there may be a mutualism between honey-hunters and beekeepers. Beekeepers might benefit from honey-hunters (who interact most with honeyguides) since honey-hunters might help sustain large honeyguide populations and encourage high levels of guiding behavior from honeyguides. Second, honey-hunters could also benefit from beekeepers since they can pretend (to law enforcement authorities such as park rangers) to be beekeepers so that they can get access to honey-hunting in protected areas. Consistent with that idea, I found that many (25%) of my respondents carry out both beekeeping honey-hunting rather than being specialised on just one activity. Third, honeyguides could benefit from both honey-hunters and beekeepers since both honey-hunters and beekeepers reward honeyguides with empty wax combs after being guided to wild bees' nests or beehives. Therefore, high levels of honey production by both beekeepers and honey-hunters makes wax available in the environment, and probably helps to sustain high honeyguide populations which continue to guide people in the future.

Thriving honey-hunting culture in southern Tanzania

Honey-hunting means to hunt or search for wild bees nesting in natural locations, usually holes in trees. Human honey-hunters often cooperate with honeyguides to find wild bees, because it is difficult for humans to find these concealed nest locations (Isack & Reyer, 1989; Wood et al., 2014). Honey-hunting in protected areas such as Forest Reserves is illegal in southern Tanzania because of its perceived negative impact on causing wildfires (Andrew, 2022).

I found that despite this, honey-hunting culture is still thriving in southern Tanzania, and honey-hunters often interact with honeyguides to find wild bees (Figure 10). In northern Tanzania (to the north of my study area) and in northern Mozambique (to the south of my study area), other cultural groups such as the Hadzabe, Ndorobo, Sonjo, Maasai and Yao people also regularly cooperate with honeyguides to find wild bees (Laltaika, 2021; Spottiswoode et al., 2016; Wood et al., 2014). Many honey-hunters in southern Tanzania anecdotally mentioned that their harvesting yield is increases when they cooperate with honeyguides; for example, describing that they can harvest up to 100 litres of honey per day with the help of honeyguides, whereas only get a gin bottle's worth of honey (honey is commonly sold in gin bottles) without the help of honeyguides.

A very interesting finding was that across all four regions I surveyed, 59% of honey-hunters reported having been guided to stingless bees (*Hypotrigona* spp.). This is rare across most of Africa; in most places honeyguides only guide people to honeybees despite people often being interested in harvesting stingless bees too (reviewed by Cram et al., 2022), with the exception of northern Mozambique, 500 km south-east of my study area, where honeyguides also regularly guide people to stingless bees' nests (Spottiswoode et al., 2016). The reasons for this variation are unknown.

Human-honeyguide signals used in southern Tanzania

I investigated the sounds used by honey-hunters in southern Tanzania, because many honey-hunting cultures in sub-Saharan Africa have developed their own signals or calls to attract honeyguides, and to communicate with honeyguides while following them to the bees' nests; these can comprise vocal sounds or whistled melodies (Isack & Reyer, 1989; Spottiswoode et al., 2016; van der Wal, Gedi, et al., 2022; Wood et al., 2014). I found that like elsewhere in Africa, honey-hunters in my study area also used a specific call or specialised signals to interact and communicate with honeyguides to find wild bees. Also, like in some other studies (Laltaika, 2021), I found that honey-hunters used different calls for the two phases of a honey-hunt: the first phase is to attract honeyguide (these signals are referred to as 'attracting calls'), and second phase is to convince and maintain the honeyguide's attention while following a honeyguide to a bees' nest (these are referred as 'coordination calls').

The specific calls that honey-hunters used to communicate with honeyguides differed between different cultures or groups of cultures, but were highly consistent within them. First, Hehe honey-hunters in the Iringa region reported that they use "rrr rrr" or combination of "rrr rrr" and whistling as attracting calls. These "rrr rrr" sounds are remarkable for sounding very similar to the ''brr-hm'' calls used by Yao honey-hunters in northern Mozambique (Spottiswoode et al., 2016), about 500 km to the south-east of Iringa. Second, Kimbu, Sangu, and Ngoni honey-hunters in Rungwa reported that they use "prrr prrr mama" and spoken words as attracting calls; again the "prrr" sound is very similar to the 'brrr' of the 'brrr-hm' used in northern Mozambique. Third, Nyamwezi honey-hunters in Tabora, and Konongo honey-hunters in Katavi, reported that they used "prrr prrr mama" or "liga liga mama" and spoken traditional words as attracting calls.

Coordination calls given while following honeyguides often involved spoken words from their local language and whistling; the meaning was often to convince and express their humble feeling to honeyguides who know the location of wild bees. For example, Konongo, Kimbu, Sangu, Ngoni and Nyamwezi honey-hunters in Rungwa, Katavi and Tabora reported using words ("prrr prrr mama", meaning "please my mother guide me"), mixed with "liga liga", meaning "please help me mama", and then sing traditional songs continuously. The songs often included words with the following meaning:

"*Please mama,*
Your child is hungry,
Guide me to the honey,
My mother helps me to find honey for my family,

I can't see without your help".

This reflects the different uses of honey: people ask honeyguides to show them honey because they need something to eat, and also express that they need honey for their family, which means they need to get honey to sell.

Human traditions of rewarding the honeyguide

Honey-hunters in some places in Africa often reward honeyguides with or empty wax combs/wax combs containing bee brood, as a sign of gratitude and to encourage the honeyguide to guide them again (Isack & Reyer, 1989; Spottiswoode et al., 2016). However, other honey-hunting cultures bury or burn empty wax: for example, Hadzabe honey-hunters in northern Tanzania do not reward the honeyguide, with the intention to keep the honeyguide hungry so it guides them to other bees' nests (Wood et al., 2014).

In southern Tanzania, I found that the honey-hunters overall did leave bee products (empty wax combs and brood) as reward for the honeyguides when harvesting honeybees' nests (Figure 10), though not stingless bees' nests. Interestingly, in this region these same honeybee bee products are also used by many honey-hunters, who use empty wax combs to make purified wax to sell, and use bee brood as food for men. Therefore this reward might come at a cost to the honey-hunters. This contrasts with northern Tanzania and northern Mozambique where empty wax combs are not used by honey-hunters (Laltaika, 2021; Spottiswoode et al., 2016).

There were some interesting variations to this general pattern. One Gogo respondent reported that he often not does reward the honeyguide for the first time after honey-harvesting, so that the honeyguide leads him to more bees' nests, and only at the end does he reward the honeyguide, when he has more to harvest. Five Hehe honey-hunters in Iringa reported that they don't have legal access to honey-hunting in protected areas, so when sneaking in to honey-hunt in protected areas, they don't reward honeyguide up front, and instead lead the honeyguide to come outside the protected area and eat leftovers on the ground after squeezing the honey.

As noted above, all 32 beekeepers who mentioned that they interact with honeyguide (to find which hive is ready to harvest) also reported that they reward honeyguides with few empty wax combs.

Interestingly, all respondents had a positive view of the necessity of rewarding the honeyguide: 53% of honey-hunters reported that it is essential to reward honeyguides with empty wax combs because it encourages the honeyguide to continue to guide and show more bees' nests, and 44% reported that it is traditional to reward honeyguides because they depend on wax to eat as food.

Ecosystem effects of honey-harvesting in southern Tanzania

I found that honey-harvesting in southern Tanzania probably has ecosystem effects on bees, trees, fire, and other wax-eating animals.

Effects on bees occur through stress during the honey harvesting process, loss of honey supplies, and colony movements prompted by harvesting. However, the scale of beekeeping implies that it probably creates a higher density of bee colonies in the environment than would naturally be the case, at least if availability of nesting sites limits bee densities in this region.

Effects on trees are typically thought to be caused mainly by honey-hunting, since to harvest honey from natural nest sites in trees, honey-hunters usually completely cut down the tree (Figure 11 B). However, my findings suggest that beekeeping also has effects on trees. Most beehives used by beekeepers are constructed from local trees (Figure 10 A&C). Beekeepers reported that they have on average 75 bark cylinder hives and 176 solid wood hives, both sourced from local trees and lasting 2–5 years. A back of the envelope calculation suggested that an average beekeeper would therefore need to cut down approximately 13 trees per year for beehive manufacture. Therefore beekeeping may have at least as big an effect on cutting down of trees as honey-hunting does, and perhaps even a larger effect given the scale at which beehives are produced. Whether either effect is big enough to have an important impact on tree populations is not yet known in this region. This expected large impact contrasts with a previous study from northern Mozambique where beekeeping is currently limited in reach and where traditional bark cylinder beehives were reported to last for up to 5–10 years, and so was considered to have less impact on tree populations than honey-hunting (Ribeiro et al. 2019). These impacts were estimated per unit area (0.06 trees/km^2/year) rather than per capita (13 trees/person/year) in my study, so are not directly comparable without further data.

The methods used to subdue bees also influence the effect of honey harvesting on the ecosystem. I found that these methods varied. Honey-hunters typically used an open fire to generate smoke to subdue honeybees and prevent them from stinging, whereas beekeepers mainly used an enclosed smoker and a bee suit to prevent stings. The latter presumably reduces the risk of accidental wildfires.

Honey-harvesting affects other wax-eating animals (Lloyd-Jones et al., 2022). Honey-hunters typically leave empty wax combs for honeyguides. Beekeepers use fresh wax combs to manufacture processed wax, but also leave a few combs specifically for honeyguides to eat; these can be either empty wax combs or wax combs from which the honey has been squeezed out. In addition, the “manure wax” (the dirty leftovers after wax has been purified for selling, comprising larval cocoons, propolis and other residue; this is called “slumgum” by beekeepers in Europe and North America) is dumped on the ground next to beekeeping camps. My two camera traps showed a genet and various other bird species (besides honeyguides) eating from a pile of “manure wax”, though these birds were more likely eating invertebrates attracted to it. In northern Mozambique, other animals have been observed eating wax combs left for honeyguides by honey-hunters, especially baboons, mongooses (in the same family as genets) and honey badgers (Lloyd-Jones et al., 2022). Interestingly these were also the three most commonly mentioned species reported by my interview respondents to eat wax (Figure 12). In summary, both wax combs and manure wax affect food availability to other animals in the environment.

What is the future of human-honeyguide interactions in southern Tanzania?

The relationship between humans and honeyguides is likely to be ancient (Wrangham, 2011). However, relationship is likely to change through space and time. It has been suggested the human-honeyguide relationship will perish if people no longer follow honeyguides to the bees’ nests’ (Isack, 1999).

In my study, I found that some cultures, such as Gogo, Hehe, Kimbu, Konongo, Ngoni, Nyamwezi, Nyiha and Sangu people, appear to be still active honey-hunters and so are continuing to regularly cooperate with honeyguides. However, they are facing threats to honey-hunting, which may dim their ability to honey-hunt in the future. Restricted access to protected areas means that honey-hunting persists largely as an illegal activity. The majority of honey-hunters mentioned that they are traditional honey-hunters in their villages and that their livelihoods are dependent on hunting honey, so they sneak illegally into protected areas to honey-hunting. Some respondents (and particularly people who both honey-hunt and keep bees) mentioned that they pretend to be beekeepers so that they can get access to honey-hunting areas, since the government gave forest land to beekeepers to support beekeeping projects. This has led to some honey-hunters altering or not using the traditional call they would normally use to attract honeyguides.

Interestingly, I learnt that even beekeepers interact with honeyguides, to find which among their hundreds of hives are ready to harvest. This may result in a high frequency of human-honeyguide interactions, since many people are motivated to keep bees given the high demand for honey production and beekeeping being encouraged by NGOs and government. Conversely, some interview respondents thought that the human-honeyguide relationship will decrease over time, due to (i) habitat loss and climate change which leading to the reduction of bees and honeyguides population over time; (ii) restricted access to protected areas where honey-hunting is illegal; (iii) a loss of interest in following honeyguides, due to honey-hunting culture being lost because people are more educated and employed; and (iv) beekeeping replacing honey-hunting since beekeeping projects are encouraged by NGOs and government. Similar concerns have been shared by honey-hunters in northern Tanzania, where Hadza and Ndorobo honey-hunters commented that climate change effects on bee habitat and the expansion of agriculture areas and human settlement will likely reduce human-honeyguide interactions in the future (Laltaika, 2021).

Overall, in southern Tanzania the picture is mixed, but in the medium term we have reasons to hope that human-honeyguide interactions will continue to exist in this region.

Conclusions

My results shows that mutualism between honeyguides, beekeepers, and honey-hunters is still thriving in southern Tanzania. Gogo, Hehe, Kimbu, Konongo, Ngoni, Nyiha, Nyamwezi and Sangu people still actively practice honey-hunting with honeyguides. Moreover, beekeepers use honeyguides to find which among their many hives are ready to harvest, and then specifically reward the bird with empty wax combs. Honey-hunting is forbidden from protected areas such as Forest Reserves and National Parks, and regarded as poaching for forest resources. Honey-hunting benefits both honeyguides and people; honey-hunters depend on honey to sell, to use as food, to use in ceremonies such as traditional weddings, and as medicine for ulcers and cough. It is therefore important for honey-hunting to continue since it supports both human and bird livelihoods.

I suggest that honey-hunting should be permitted in Forest Reserves and given similar priority as beekeeping projects. I also suggest that beekeeping projects should continue to be encouraged, since they also benefit both people and honeyguides, but that beekeepers should ideally use other type of hives such as top bar hives or clay hives, rather than depending on bark or log hives which involve felling large numbers of local tree species. The honey-harvesting methods used by beekeepers (e.g. the use of bee suits, and cassava leaves to subdue bees, that reportedly reduce bees' desertion) already have less ecosystem impact than using open fires to generate smoke to subdue bees. Taken together these measures will help to ensure that both humans and birds continue to benefit from cooperation, while also reducing its impacts on the environment.

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Appendix 1

The selection of interview questions to honey-hunters and beekeepers that were asked and analyzed in this research.

GENERAL QUESTIONS

- Age
- Gender
- Cultural groups
- Livelihood(s)

HONEY USE

- Do you use honeybee honey?
- If yes, what do you use honeybee honey for?
- Where do you get your honeybee honey?
- What is the market price for honeybee honey in your village?
- Do you use stingless bees honey?
- If yes, what do you use stingless bees honey for?
- What is market price for stingless bee honey in your village?
- Do you know the bird that guide people to honeybees' nests?
- What other animals eat wax?

HONEY-HUNTING EXPERIENCE

- Do you go on trips only for honey-hunting, or do you mainly honey-hunt opportunistically while busy with other activities like herding cattle?
- What are the best three months of the year for honey-hunting?
- How important is selling honey and/or wax for you as a source of income in the honey-hunting high season?
- Where did you learn to honey-hunt?
- When was the last time you went on a honey-hunt?
- Do you routinely go on honey-hunts by yourself, or with friends and/or family?

- When you harvest a wild bees' nest, what do you take out from the bees' nest?
- When you harvest a wild bees' nest, what do you use from the harvest? What do you consume at the site, and what is taken home?
- Do you use honeyguides to find bees' nests?
- Do you ever leave things for the bird to eat after being guided to a bees' nest? If yes, why?

HONEY-HUNTING SIGNALS

- Do you use sounds to communicate with the honeyguide?
- Does the sound you use differ when you are calling in the bird, to when you are following it? If yes, how does it differ?

OTHER HONEYGUIDE BEHAVIOUR

- 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 leave a reward for the bird? Why?

HONEY-HUNTING SUSTAINABILITY

- What means to subdue bees (to prevent stinging) do you use?
- When you harvest a nest, do you do anything to encourage the bees to return to it?

TREND OF MUTUAL INTERACTION IN FUTURE

- Has the practice of honey-hunting in general changed since you were young? If Yes, how has it changed and what is the reason?
- Has in particular the role of honeyguides in honey-hunting changed over time? If Yes, how has it changed and what is the reason?
- Do you think the interaction between people and honeyguides will exist in the future?
- How do you see the interaction between people and honeyguides changing in future generations?

INTERVIEWEES WHO KEEP BEES

- What motivates you to keep bees?
- Why don't you collect honey from wild bees?
- How many of each of these types of beehives do you have?

- When you harvest a man-made hive, do you have any other means to subdue the bees from sting than use of smoke? If yes, what is the other means?
- When you harvest a man-made hive, what do you take out of the hive?
- When you harvest a man-made hive, what do you use from the harvest? If not everything, what do you do with the rest?
- How and where do you take the honey from the comb? What do you do with the empty combs?
- Do you think the interaction between people and honeyguides will exist in the future?
- How do you see the interaction between people and honeyguides changing in future generations?

Appendix 2

English version of consent script signed by all participants in this study.

Your invited to participate in research that is interested to find out more about how people obtain honey in southern Tanzania. If you are or were honey-hunter, beekeeper, or obtain honey from other sources, we would like to talk to you. The interview will take max.one hour, during which you will be asked to answer a set of questions 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 videos as a part of the study. If you are an active honey-hunter, we might ask to join you on real time honey-hunt during which we will record a video and sound, and your 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 anonymised photographs/videos in website and publications for research purposes

Name of participant	Signature or Fingerprint of participant	Date
Name of researcher	Signature of researcher	Date