Cooperation, ecology and behaviour in the honeyguide-human mutualism

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I dedicate this thesis to
the honey-hunters of Africa –
to those who call to honeyguides,
and those who listen and reply

Glory be to God for dappled things –
For skies of couple-colour as a brinded cow;
For rose-moles all in stipple upon trout that swim;
Fresh-firecoal chestnut-falls; finches' wings;
Landscape plotted and pieced – fold, fallow, and plough;
And all trades, their gear and tackle and trim.

All things counter, original, spare, strange;
Whatever is fickle, freckled (who knows how?)
With swift, slow; sweet, sour; adazzle, dim;
He fathers-forth whose beauty is past change: Praise him.

– Gerald Manley Hopkins

DECLARATION

This thesis reports original research that I conducted while enrolled as a PhD student at the FitzPatrick Institute of African Ornithology, University of Cape Town. All assistance received was in line with normal support provided by supervisors and has been fully acknowledged. This work has not been submitted in any form for any degree at any other university.

I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publication, in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publication:

Lloyd-Jones, D.J., St Clair, J.J., Cram, D.L., Yassene, O., van der Wal, J.E., Spottiswoode, C.N. When wax wanes: competitors for beeswax stabilize rather than jeopardize the honeyguide–human mutualism. *Proceeding of the Royal Society B: Biological Sciences*, 289:20221443

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ABSTRACT

This thesis explores several behavioural and ecological aspects of the human-honeyguide mutualism, a unique interspecies interaction in which greater honeyguides (*Indicator indicator*) cooperate with humans by guiding them to wild bees' nests. This mutualism enables each species to obtain a high-calorie, preferred food: wax for honeyguides and honey for humans. This foraging cooperation is an intriguing example of a vertebrate-vertebrate mutualism in which humans are half of the partnership, making it particularly tractable for study. Working with a community of honey-hunters in Niassa Special Reserve, northern Mozambique, I investigated: (1) the costs and benefits of the mutualism to both species, in relation to variation in cooperative interactions over time and space, (2) the exploitation of wax rewards by honeyguides and other wax-eating species, (3) whether and why honeyguides sometimes guide humans to animals other than bees, and (4) the impact and sustainability of honey-hunting on miombo tree ecology, and how this is influenced by honeyguides. I found, first, that human-honeyguide cooperation resulted in an increased rate of finding bees' nests for humans, from which both partners overwhelmingly gained a benefit. Interaction rates at the study site occurred over a large area and remained stable from 2017–2022 which, together with the apparently low costs of failed interactions, maintains the mutualism. Second, I found that the exploitation of wax rewards by conspecifics and other wax-eating animals did not jeopardize the mutualism, highlighting how wider ecological influences contribute to mutualistic persistence. Five mammalian and bird species recorded as wax-competitors were not previously known to consume wax. Third, I found evidence that honeyguides rarely but deliberately guide humans to animals other than bees, yet this behaviour (often culturally attributed to punishment) was not linked to prior rewarding or non-rewarding behaviour by honey-hunters. This and observational evidence best support the hypothesis that guiding to non-bee animals results from a cognitive recall error of spatial information. Lastly, I found that although honey-hunters frequently fell trees to harvest honey, at the landscape level the influence of honey-hunters on tree populations was spread over many tree species and sizes, at low densities, and that human-honeyguide cooperation likely further reduces this impact by leading honey-hunters to smaller-sized trees. This work draws together findings from several disciplines, linked by the central human-honeyguide relationship, to provide insights into how a mutualism both shapes and is shaped by ecological, behavioral, and cultural factors, and contributes to our understanding of mutualistic interactions.

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PUBLICATIONS ARISING FROM THIS THESIS

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The data published in the above paper are presented in Chapter 3 of this thesis. I have edited this chapter for consistency with the rest of the thesis, including adding references to the other relevant chapters. I made the largest contribution to the publication, including study design, field work, analysis of the data, drafting of the manuscript, and responding to reviewers' comments. All co-authors were actively involved in reviewing and revising the manuscript.

COLLABORATIVE PUBLICATIONS ON HONEYGUIDES

Throughout the duration of research for this thesis, I contributed ideas, observations, data, editing and writing to sections in all the following publications on greater honeyguides:

Cram, D.L., **Lloyd-Jones, D.J.**, van der Wal, J.E.M., Lund, J., Buanachique, I.O., Muamedi, M., Nanguar, C.I., Ngovene, A., Raveh, S., Boner, W., Spottiswoode, C.N. 2023. Guides and cheats: producer-scrounger dynamics in the human-honeyguide mutualism. *Proceedings of the Royal Society B: Biological Sciences* 290: 20232024

van der Wal, J.E.M., Afan, A.I., Anyawire, M., Begg, C.M., Begg, K.S., Dabo, G.A., Gedi, I.I., Harris, J.A., Isack, H.A., Ibrahim, J.I., Jamie, G.A., Kamboe, W.-B.W., Kilawi, A.O., Kingston, A., Laltaika, E.A., **Lloyd-Jones, D.J.**, M'manga, G.M., Muhammad, N.Z., Ngcamphalala, C.A., Nhlabatsi, S.O., Oleleteyo, T.T., Sanda, M., Tsamkxao, L., Wood, B.M., Spottiswoode, C.N., Cram, D.L. 2023. Do honey badgers and greater honeyguide birds cooperate to access bees' nests? Ecological evidence and honey-hunter accounts. *Journal of Zoology* 321: 22-32

Spottiswoode, C.N., Lund, J. & **Lloyd-Jones, D.J.** 2022. Quick Guide: Honeyguides. *Current Biology* 32: R1072-R107

Cram, D.L., van der Wal, J.E.M., Uomini, N.T., Cantor, M., Afan, A.I., Attwood, M.C., Amphaeris, J., Balasani, F., Blair, C.J., Bronstein, J.L., Buanachique, I.O., Cuthill, R.R.T., Das, J., Daura-Jorge, F.G., Deb, A., Dixit, T., Dlamini, G.S., Dounias, E., Gedi, I.I., Gruber, M., Hoffman, L.S., Holzlehner, T., Isack, H.A., Laltaika, A.E., **Lloyd-Jones, D.J.**, Lund, J., Machado, A.M.S., Mahadevan, L., Moreno, I.B., Nwaogu, C.J., Pierotti, R., Rucunua, S.A., dos Santos, W.F., Serpa, N., Smith, B.D., Sridhar, H., Tolkova, I., Tun, T., Valle-Pereira, J.V.S., Wood, B.M., Wrangham, R.W. & Spottiswoode, C.N. 2022. The ecology and evolution of human-wildlife cooperation. *People and Nature* 4: 841-855.

van der Wal, J.E.M., Spottiswoode, C.N., Uomini, N.T., Cantor, M., Daura-Jorge, F.G., Afan, A.I., Attwood, M.C., Amphaeris, J., Balasani, F., Begg, C.M., Blair, C.J., Bronstein, J.L., Buanachique, I.O., Cuthill, R.R.T., Das, J., Deb, A., Dixit, T., Dlamini, G.S., Dounias, E., Gedi, I.I., Gruber, M., Hoffman, L.S., Holzlehner, T., Isack, H.A., Laltaika, A.E., **Lloyd-Jones, D.J.**, Lund, J., Machado, A.M.S., Mahadevan, L., Moreno, I.B., Nwaogu, C.J., Pereira, V.L., Pierotti, R., Rucunua, S.A., dos Santos, W.F., Serpa, N., Smith, B.D., Tolkova, I., Tun, T., Valle-Pereira, J.V.S., Wood, B.M., Wrangham, R.W. & Cram, D.L. 2022. Safeguarding human-wildlife cooperation. *Conservation Letters* e12886

TABLE OF CONTENTS

CHAPTER 1

General Introduction

Preamble

In this chapter, I present a thesis rationale and briefly summarize the existing research literature on the mutualism between greater honeyguides (*Indicator indicator*) and humans. I then place the overarching research questions within the literature on mutualism in general, and briefly introduce the study area and study system. Lastly, I provide a thesis outline with brief overviews of each chapter. Throughout this thesis the generic term 'honeyguide' when used alone always refers to greater honeyguides, although I sometimes specifically refer to greater honeyguides where confusion with other honeyguide species may arise.

Thesis rationale

The cooperative foraging relationship between greater honeyguide birds (*Indicator indicator*) and humans (Friedmann 1955; Isack and Reyer 1989) is a system offering a compelling lens through which to examine the behavioural and spatial complexities within mutualism. Mutualism is defined as an ecological relationship where two or more species receive reciprocal benefits (Bronstein 2015). In the human-honeyguide mutualism, honeyguides innately possess the ability to locate wild bees' nests (Isack 1987) across their sub-Saharan savannah range (Figure 1.1). Honeyguides supplement their insectivorous diet with energy-rich beeswax (Diamond 1988;

Chapter 2; Cram et al. 2023), but are often limited in access to it by the aggressiveness of African honeybees (*Apis mellifera*) and by the constricted entrances to the tree cavities which many bee colonies inhabit (Isack 1987). Honey from wild bees is an ancient and important source of food for humans (Marlowe et al. 2014; Wrangham 2011), both now and over at least the past 500,000 years (Wrangham 2011) – more or less since humans have had the ability to make fire and create smoke with which to subdue bees (Gowlett 2016). These converging interests, along with human tool-use and advanced cognitive and social capabilities, make humans highly efficient partners to honeyguides (Isack 1987; Wood et al. 2014).

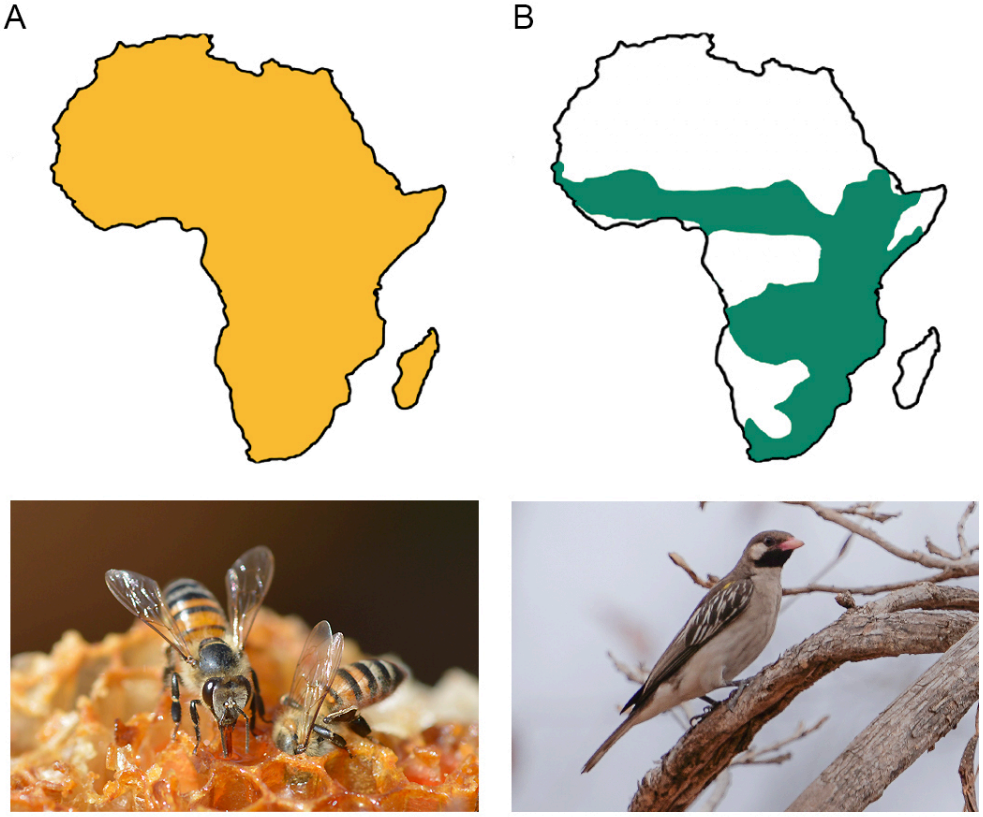

Figure 1.1. Maps of the African ranges of (A) African honeybees (*Apis mellifera*; Requier et al. 2019) and greater honeyguides (*Indicator indicator*; Fry et al. 1988).

To guide humans to bees' nests, honeyguides across Africa give distinctive chattering calls which attract the attention of honey-hunters (Friedman 1955; Isack 1987; Wood et al. 2014, Spottiswoode 2016). Honeyguides then continuously produce these calls while indicating the direction to a bees' nest by flying from tree to tree (Isack 1989). Humans are usually guided after either specifically investing energy in attracting honeyguides using culturally maintained signals of cooperation (Isack and Rayer 1989; Spottiswoode et al. 2016; Spottiswoode and Wood 2023), or else after being spontaneously approached by honeyguides attempting to guide them (Isack 1987, Short and Horne 2001). After being guided to a bees' nest, honey-hunters decide whether or not to harvest the nest using axes and smoke (Isack 1987), and in some human cultures leave behind empty pieces of honeycomb as a reward, which the nearby waiting honeyguide later descends to and eats (Friedmann 1955; Isack 1987; Short and Horne 2001). Not all human cultures have a tradition of actively rewarding honeyguides, but by subduing the bees with smoke and opening a tree cavity with tools such as axes, it is likely that humans allow honeyguides to gain scraps of wax regardless of whether humans actively choose to reward them or not (Wood et al. 2014; Laltaika 2021; van er Wal 2022a; Chapter 3). In this way, honeyguides exchange information about the location of bees to humans for access to beeswax, and sometimes also bee brood (but not honey) as food.

This specialised behaviour arises despite the fact that honeyguides are brood parasites (see "The biology of the greater honeyguide", below), so they are raised by other species and have no direct opportunity to learn from their parents. The specific role of learning and experience versus innate behaviour in honeyguides is not well understood. The tendency in honeyguides to approach humans appears to be innate, and juveniles that have likely never guided a human (or seen another honeyguide do so) will approach humans and attempt to guide them (Short and Horne 2001; pers. obs.). Similarly, honeyguides in places where they are likely to have no prior experience of humans still approach people and spontaneously give the chattering call, strongly suggesting an innate basis for attempting to guide (Short and Horne 2001). In some locations, honeyguides preferentially approach humans in response to a local call or signal of cooperation, and this preference is likely learnt, although it is unclear whether recognition is acquired through social learning or solely through individual experience (Wood et al. 2014; Spottiswoode et al. 2016; Spottiswoode and Wood 2023).

Whilst guiding, honeyguides often fly directly towards a bees' nest (Isack 1987; Spottiswoode et al. 2016), strongly suggesting that the precise locations of bees' nests within the local environment (and navigation towards them) is learnt and not innate. Honeyguides also alter their chattering call when they arrive in the vicinity of bees' nest (Isack 1987). This behaviour is likely to innate, yet the specific role of learning in this behaviour is not known. Finally, many species of honeyguide (including greater honeyguides) appear to be instinctively attracted to beeswax (Fry et al. 1988), perhaps through olfaction (Stager 1967), as in the lesser honeyguide, *Indicator minor* (Parker 2018).

For such an intriguing human-animal relationship, the entire scientific literature on guiding behaviour by greater honeyguides is not as extensive as one may expect. Greater honeyguides and their behaviour of guiding humans to bees was first formally described in the scientific literature by Sparrman (1777). Guiding behaviour, however, was reported in print as far back as 1609 (dos Santos, 1609) and regularly throughout Africa until the twentieth century (Ludolphus, 1682, da Sorrento, 1744; Delegorgue, 1847; Cumming, 1856; Livingstone, 1857), but has likely been known to Indigenous sub-Saharan human cultures for millennia (Isack, 1987; Wrangham, 2011; Cram et al. 2022). Many of these early published accounts were not first-hand observations, and unfortunately missed key information about the details of guiding interactions.

Livingstone's first-hand reports were notable for reporting both how frequent successful guiding interactions were across much of East Africa, and also for observing how abundant honeyguides were in northern Mozambique ("The honey-guides were very assiduous in their friendly offices, and enabled my men to get a large quantity of honey"), in the same area as where research for this thesis took place (Livingstone 1857). In the first half of the twentieth century, a number of published remarks on honeyguides were made but added little new to our understanding of guiding behaviour, other than expanding the known geographic distribution of human-honeyguide interactions (Percival 1924; Hoesch 1937; Chapin 1939; Skead 1951; Ionides 1965; Carr 1969; Ville 1995). It was Herbert Friedmann, in his 1955 monograph '*The honey-guides*' (Friedmann 1955), who provided the first synthesis of knowledge on both honeyguide breeding biology and guiding behaviour. Friedmann was also likely the first to draw considerable attention to guiding behaviour to an audience outside Africa, due to a widely-read popular publication (Friedmann 1954).

The most comprehensive research (and first PhD) to greatly advance our understanding of guiding behaviour by honeyguides was conducted by Hussein Isack, working in northern Kenya (Isack 1987). In his ground-breaking studies, he showed that honeyguides can provide reliable information about the location of bees' nests to their human partners, that honeyguides can guide to bees' nests over a wide range of distances, and that honeyguides primarily use acoustic signals to guide humans (although visual cues are also often used as well). He also showed how guiding honeyguides appear to alter their acoustic signals with proximity to a bees' nest (Isack 1987; Isack and Reyer 1989). He also thoroughly documented the anthropology and natural history of honey-hunting by the Boran people and their cultural relationship with the honeyguide (Isack 1987), and how this relationship is threatened by cultural change (Isack 1999).

Following this, Diamond and Place (1988) provided further confirmation about wax consumption and digestion by greater honeyguides. Dean et al. (1990) discussed why honeyguides are unlikely to guide honey badgers (*Mellivora capensis*) to bees, as well as the persistence of the mutualism in a changing continent. Short and Horne (2001) added first-hand observations from Kenya, particularly on the natural history of wax-eating, to an updated synthesis of honeyguide biology. In northern Tanzania, Wood et al. (2014) neatly added to Isack's work by describing and measuring the interactions and payoff rates between Hadzabe hunter-gatherers and honeyguides. Wood et al. (2014) reported that unlike some other human cultures, Hadzabe honey-hunters hide, bury, and burn wax comb following harvests with the intent of keeping the bird hungry and thus more likely to guide again. Spottiswoode et al. (2016) added to this by experimentally showing how in northern Mozambique (at the same site as the research from this thesis), local sounds used by Mozambican honey-hunters increase the probability of being guided by a honeyguide, and thus the probability of finding a bees' nest per unit time of searching.

In the Adamaoua region of Cameroon, Gruber (2018) found that while human-honeyguide cooperation persists, demand for higher quality honey has caused an increase in beekeeping and a decrease in the harvests of wild bees' nests, and therefore a decrease in human-honeyguide interactions. In northern Tanzania, Laltaika (2021) studied honeyguide-human interactions across four cultures (Hadzabe, Ndorobo, Maasai, Sonjo) and found that in areas where the mutualism still thrives, the calls used to recruit honeyguides are largely consistent within cultures but different amongst cultures. In eastern Kenya, van der Wal et al. (2022a) also reported that another honey-hunting culture, the Awer, still cooperate with honeyguides, but in that region honey-hunting activity is rapidly declining.

Using a subset of the spatially-explicit honey-harvest data collected for this thesis (Chapter 2) from northern Mozambique, Cuthill (2023) linked fire ignitions in Niassa to satellite imagery of fire ignitions to determine the proportion of honey-hunter linked fires to those lit by management authorities, and therefore the ecological impact of honey-hunting on the landscape via fire. From 2017 to 2021, he found that only 1.47% (n = 54) of fires in the landscape could be linked to honey-hunting activity, more than half of which burned in the early dry season months

(May to June). These earlier fires, and management fires lit in the same period, were better at creating firebreaks and therefore likely lead to a reduction in the severity of subsequent fires, supporting existing management practices in Niassa which prioritise early burning.

In southwestern Tanzania, Kilawi (2023) found that beekeepers with hundreds of hives spread out in extensive woodland areas use honeyguides to more efficiently find active beehives for harvest. These beekeepers reportedly reward honeyguides with wax following cooperative interactions, making this interaction mutualistic and maintaining rather than undermining the honeyguide-human relationship. In Cram et al. (2023) we reported how individual honeyguides flexibly switch tactics between guiding and scrounging behaviour, and that guiding yielded greater access to beeswax, which in turn likely supports cooperative versus scrounging behaviour by individual honeyguides. Spottiswoode and Wood (2023) experimentally demonstrated that honeyguides in northern Tanzania and northern Mozambique discriminate among honey-hunters' calls, responding more readily to local than to foreign calls used to attract them. Their results suggest that honeyguides learn the locally varying signals of their local human partners. Most recently, M'manga (2024) found that human-honeyguide cooperation is still active in northern Malawi, yet honey-hunting activity in that region is also declining.

Alongside this growing body of empirical research on honeyguide-human mutualism, there have also been four recent review papers on greater honeyguides. First, in Cram et al. (2022), we reviewed and contrasted the human-honeyguide mutualism with other forms of human-wildlife cooperation (especially human-dolphin cooperation; see Cantor et al. 2023) and proposed potential evolutionary origins for these unique cooperative interactions. We distinguished between human-wildlife mutualisms, which are ecologically and economically important mutually beneficial relationships between humans and wildlife (e.g., bats that eat insect pests attracted to houses or species which pollinate crops; Ghanem and Voigt, 2012; Kremen et al. 2004) and human-wildlife cooperation, which is specifically defined by coordinated cooperative behaviour. Human-honeyguide cooperation can be considered one specific example of human-wildlife cooperation. In this thesis, I do not use the alternative definition of 'cooperation' which limits it to mutual helping between members of the same species, and applies 'mutualism' only between unrelated species (Lehmann and Keller 2006; Bronstein, 2015). Whilst this is an important distinction, the human-honeyguide relationship is both mutualistic and cooperative, and by describing the human-honeyguide interactions as 'cooperative' I emphasize the active, coordinated aspects of these behaviours.

Second, in van der Wal et al. (2022b), we reviewed the risks that the honeyguide-human mutualism (and other human-wildlife cooperative relationships) face and made recommendations for safeguarding them. Third, in Spottiswoode et al. (2022), we briefly reviewed many aspects of honeyguide biology. Finally, in van der Wal et al. (2023) we reviewed the evidence that honey badgers and honeyguides cooperate to find bees' nests, drawing from the published literature, from direct observations, and from interviews with honey-hunters in 11 communities in nine African countries. No scientific evidence was found to convincingly indicate that honey badgers and honeyguides cooperate, yet reports of this occurring from three adjacent cultures in Tanzania suggests that the interaction may occur, but is highly localized and extremely difficult to observe.

To this body of literature, I add this thesis. I directly address three questions highlighted in Cram et al. (2022) as important research directions: What are the quantitative benefits of participating in the mutualism for the wildlife partner, relative to non-participation? What are the costs of involvement in human-wildlife cooperation for both species? What are the impacts of human-wildlife cooperation on the local ecological community?

Contribution to knowledge

Humans are unable to coerce honeyguides into guiding them to bees, simply because honeyguides are free-living birds, not physically restrained or controlled by humans. This means that honeyguides have the agency to decide whether or not to cooperate, and with whom. Such flexibility is distinctly different to that observed in examples of coerced human-animal cooperation such as between humans and dogs (*Canis lupus*) or golden eagles (*Aquila chrysaetos*) used for hunting (Koster 2008, Bautista-Rodríguez and Ellis 2024), or cormorants (*Phalacrocorax* spp.) and otters (various *Lutra* spp.) used for fishing (Gudger 1927; Manzi and Coomes 2010; Feeroz et al. 2011). In contrast to these examples, the human-honeyguide mutualism arose through natural selection and therefore provides an intriguing opportunity to observe how the mutualism is naturally maintained in response to the behaviours of the participants and the spatial distribution of resources (Jones et al. 2015). It also provides an opportunity to better understand how human-wildlife cooperation (and mutualisms in general, see next section) persist despite the ever-present risk of the overexploitation or abandonment of one partner (Ferriere et al. 2002, Sachs and Simms 2006).

Some of these broad questions were addressed by Hussein Isack's groundbreaking research in the 1980s. However, his work preceded the availability of handheld GPS (Global Position System) and modern spatial analyses. These tools now provide a new opportunity for investigating questions regarding the stability of the human-honeyguide mutualism in much greater spatial detail than prior studies. For example, technological advances (such as a custom-made icon-driven application loaded onto smartphones) enabled us to implement a unique system in which illiterate or semi-literate honey-hunters, and so first-hand participants in the human-honeyguide mutualism, were able to collect reliable behavioural and ecological data on human-honeyguide interactions over five years (2017–2022). This dataset specifically allowed the quantification of some of the costs and benefits associated with honey-hunting for both partners, and enabled us to link these dynamics to honey-hunting outcomes (the focus of Chapter 2).

Knowledge gaps in how the honeyguide-human mutualism affects (and is affected by) the local ecological context and behaviour of both species were the focus of camera-trapping and audio recording of cooperative interactions. I was able to monitor feeding visits to wax comb made available following honey harvests and so better understand the competitive dynamics directed towards honeyguides. A five-year dataset collected by honey-hunters on trees containing bees' nests enabled a detailed exploration into the ecosystem effects on trees of guiding behaviour and of human honey-gathering at the landscape level (the focus of Chapter 5).

The ecology and evolution of mutualism

Mutualisms, where two or more species receive reciprocal benefits, are a fundamental ecological relationship underpinning biodiversity, ecosystem functioning and nutrient cycling across the globe (Klein et al. 2007; Bronstein 2015). Such relationships are everywhere (Bronstein 2015) and range from plant–bacterial mutualism, which generate an estimated 60% of annual terrestrial nitrogen input (Zahran 1999), to marine coral-algal interactions (Mogen and Folke 1999), plant-pollinator mutualisms (Pellmyr 2003, Janzen 1979) and terrestrial ant-plant mutualisms (Palmer 2008, Kamaru et al. 2024). Studies across a wide range of empirical and theoretical mutualistic systems have sought to understand the persistence of mutualisms despite competition (Johnson and Bronstein 2019; Jones et al. 2012), variation in the spatial distributions of partners, and variation in the costs and benefits within cooperation (Ferriere et al. 2002, Herre and West 1997; Herre et al. 1999).

Table 1.1. Mutualism can be defined as the collective action of two populations where each population, at a cost to themselves, produces benefits that reduce the other's stress. Here, the benefits, costs and stressors for the honeyguide-human mutualism are contrasted to some other mutualisms. Although stress to humans or honeyguides is not explicitly measured in this study, consideration of the underlying stressors influencing mutualistic outcomes underpins a more complete understanding of mutualistic dynamics (following Wu et al. 2019).

Type of mutualism	**Partner**	**Benefit**	**Costs**	**Stress**
Nutritional mutualism	Human	Access to energy-rich food (honey)	Energy expended while being guided and harvesting honey Energy expended moving into optimal foraging areas	Starvation/ energy depleted environment
	Honeyguide	Access to energy-rich food (beeswax)	Possible risk of predation while guiding (Cram et al. 2022) Energy loss while guiding Energy expended searching for bees' nests (presumed)	Starvation/energy depleted environment
Nutritional mutualism	Corals	Higher rate of calcification and conservation of nutrient (Muscatine and Porter 1977)	Reduced cover, growth and fecundity (McCook et al. 2001)	Nutrient-poor marine environment
	Algae	Better habitat and increased availability of inorganic compounds (Wooldridge 2010)	Energy loss, possible restricted growth by coral (Wooldridge 2010)	Nutrient-poor marine environment
Transportation mutualism	Plants	Increased fecundity (Christian and Stanton 2004)	Seed consumption and energy loss (Pyke 1991)	Limited spatial range for reproduction
	Seed dispersers or pollinators	Access to nutrient-rich food	Energy loss or by-product mutualism	Starvation
Protection mutualism	Plants	Increased fitness due to reduced consumption from herbivores (Kamaru et al. 2024)	Energy loss or by-product mutualism	Consumption by herbivores and competing plants
	Ants	Increased access to nutrients and shelter (Palmer 2008)	Energy loss or by-product mutualism	Lack of suitable nesting sites (Heil and McKey 2003)

Although many mutualisms have been well studied under controlled or isolated *ex situ* conditions (e.g. between plants and mycorrhizae; Kiers et al. 2011), to better understand the stability and selective dynamics of some mutualisms, it is informative (as well as necessary) to study mutualistic partners and their competitors in their natural ecological setting (Jones et al. 2012, Chomicki et al. 2020). This is because the mechanisms by which mutualisms are resilient to exploitation from non-mutualists are highly diverse (Chomicki et al. 2020). Species which form mutualistic partnerships are directly and indirectly affected by other species within their ecological community (Palmer et al. 2015), and competition towards mutualists by third-party species is often highly influential in shaping the ecology and dynamics of mutualisms (Jones et al. 2012; Bronstein 2001b; Chamberlain et al. 2014).

Mutualisms are expected to be more stable (defined as the ability of a system to return to its previous equilibrium after disturbance; May and McLean 2007) when mutualistic partners are more abundant, and under conditions of flexible partner choice (Bronstein, 2015). This is, for example, because high partner densities increase encounter rates, such as increased pollinator visits when flower densities increase (Hale et al. 2021, Morris et al. 2010). Conflict between mutualistic partners is expected to be minimal when cooperative behaviour is self-serving and the partner benefits from by-product resources. A classic example of this is when cleaner fish feed on ectoparasites of client fish, benefiting themselves while aiding the client fish (Sachs et al. 2004; Bshary et al. 2016). Theoretically, exploitation by non-mutualists should destabilize mutualisms, or even drive one of the partners extinct through competitive exclusion (Ferriere et al. 2002; Sachs et al. 2006). Nonetheless, many mutualisms persist or even thrive despite exploitative behaviour, potentially due to wide variation in the costs placed on mutualists by exploiters, and due to the specific defensive mechanisms which mutualists have evolved against exploitation (Kiers et al. 2011; Frederickson 2017; Chomicki et al. 2020).

Mutualistic species partnerships are not always beneficial to both partners at all times (Bronstein 2001b), and one partner may fail to provide the reward that the other expects (Clutton-Brock and Parker 1995). This can cause the costs of engaging in mutualistic behaviour to outweigh its benefits, such that the other partner fails to reciprocate or perhaps even punishes its partner (Riehl and Frederickson 2016). In the human-honey mutualism, one partner sometimes fails to do their part: humans may fail to harvest the nest or, having harvested the nest, fail to reward the bird, and a guiding honeyguide sometimes fails to show a human a bees' nest (Spottiswoode et al. 2016; Wood et al. 2014). Sometimes it may show a human nothing, and rarely it may guide to other animals just as dangerous to humans as honeybees. Centuries of African Indigenous accounts have intriguingly reported that honeyguides occasionally guide humans to non-bee animals, typically large animals dangerous to humans (Friedmann 1955; Isack 1987). This is interpreted by some human cultures as punishment for prior failure to reward the bird, and by others as an altruistic warning behaviour. Punishment in nature (where one partner sacrifices payoffs from an interaction to harm a cheating partner) has rarely been observed amongst non-human animals (Jensen 2010; Raihani and Bshary 2019; Raihani et al. 2012), but is known from client-cleaner fish mutualisms (Bshary and Grutter 2005). In Chapter 4, I weigh the evidence for the hypothesis that guiding to non-bee animals could indeed be punishment behaviour by honeyguides and contrast it with four alternative hypotheses.

The field of mutualism biology involves a spectacular array of field systems (Bronstein 2015), ranging from bacterial systems, bacterium-plasmid associations, plant-rhizobium interactions (Bergstrom et al. 2003) to client fish-cleaner (Bshary et al. 2016) and ant-plant systems (Pierce et al. 2000). The honeyguide-human system offers a unique opportunity to study a mutualism which is different in a number of ways from most other mutualistic systems: first, it is a vertebrate-vertebrate mutualism in which humans are one partner, making it particularly tractable for manipulating the mutualism to clearly see how and when it succeeds or fails. Second, it takes places on a spatial scale and uses sensory systems which we can readily perceive. Third, unlike for many other systems (Bronstein 2015), it is possible to quantify mutualistic investment as well costs for participating humans, and to a large degree the benefits for honeyguide as well, leaving us with only the challenge of estimating the costs to honeyguides (Chapters 2 and 4). Finally, our field-based system also allows us to explore the effects of ecological context (e.g., competitors) on the mutualism (Chapter 3) and also, conversely, the effects of the mutualism on the broader landscape (Chapter 5).

The honeyguide-human relationship can be defined as a pseudo-reciprocal mutualism in which an initial behavioural investment is required (guiding by a honeyguide) to enable a recipient (a honey-hunter) to perform a self-serving act (harvesting a bees' nest), which in turn benefits the investor (the honeyguide) as a by-product (Bshary and Bergmüller 2008). It is also a nutritional mutualism (see Table 1.1) broadly comparable to other nutritional mutualisms in which one species provides a mutualistic partner with a resource or behavioural service (e.g., pollen transport between flowers) in exchange for a food reward (e.g., nectar) which reduces the impact of an underlying stressor such as energy depletion (Jones et al. 2012; Bronstein 2015; Wu et al. 2019). Honeyguides benefit from both beeswax left behind (either deliberately or accidentally) after humans harvest a wild bees' nest, and/or simply from access to the tree cavities containing remaining pieces of wax (Isack 1987; Wood et al. 2014; Figure 1.2). Humans benefit from cooperation with honeyguides by gaining information about the location of bees, and so from honey (if they choose to harvest).

How did human-honeyguide mutualism first evolve?

The evolutionary history of this mutualism is speculative, but we can tentatively sketch out possible scenarios. We know that when one individual (in this case a honeyguide or human) receives automatic byproduct benefits from another individual (in this case the human gains knowledge of where a bees' nest is located and the honeyguide gains access to wax), natural selection can favour adaptations in either or both species to maximize these benefits (Thompson 1994). Humans have foraged for honey for many thousands of years in Africa (Crane 1999, Wrangham 2011), as likely did our hominin ancestors (Wrangham 2011). Prior to cooperative guiding interactions arising, honeyguides would likely have befitted from the harvests of bees' nest by humans – either from the subduing of bees with fire and smoke and/or from the enlarging of bees' nest entrances, through which access to beeswax was made possible. Honeyguides would therefore have recognized humans as beneficial to them and received byproduct benefits despite humans acting entirely in their own self-interest.

We could speculate that guiding behaviour itself may have arisen by two hypothetical routes, briefly summarized here: in the first hypothesized route, honeyguides scrounging wax from the messy aftermath of honey-harvests may have learnt to associate humans (or hominins) with such feeding opportunities, and then begun following hominins in anticipation of wax comb being made available (Wood et al. 2014). Then, as hominins became more adept at opening and fully exhausting the contents of *Apis mellifera* nests, scrounging behaviour in honeyguides would have been selected against and guiding behaviour in honeyguides selected for (Wood et al. 2014), establishing the reciprocal signalling and guiding-following behaviour we observe today.

In the second hypothetical route by which guiding may have arisen, the presence of honeyguides near cryptic bees' nests may have initially provided humans with a cue to the location of honey. This is very similar to the first hypothesis but rather than starting with honeyguides attending to human cues, humans also attend to honeyguide cues, resulting in an initial byproduct mutualism with only passive cues and no coordination. A mutualism based on cues is plausible since several other non-guiding honeyguide species in the *Indicator* genus are typically cryptic *except* when near bees' nests, and are used by humans as cues with which to locate bees' nests (Archer and Glen 1969). Himalayan honey-hunters for example, also use yellow-rumped honeyguides (*Indicator xanthonotus*) as cues of the locations of bee nests (Umesh Srinivasan in litt. to Claire Spottiswoode).

We might speculate that at first, honeyguides began attracting humans (or hominins) to bees using sounds produced only at bees' nests. Skead (1951) first noted the similarity between the begging calls of nestling honeyguides and the guiding calls of adults. These adapted, 'begging', food-associated calls directed towards humans in the presence of bees may have increased rates of finding bees' nests, and consequent selection towards honeyguides producing such calls. Continued cooperation (and wax benefits gained) could have also simultaneously led to the innate attraction towards humans observed in greater honeyguides to this day (Isack 1987; Short and Horne 2001). Following this, honeyguides may have started to produce these 'guiding-begging' calls upon encountering humans (not just at bees) and then flying or 'backing up' in the direction of the bees. Under this scenario, vocal signalling towards humans would have arisen prior to the physical guiding of humans by flying in the direction of the bees, tail-fanning and dipping flight.

If the idea that birds can 'guide' a human *towards* a predetermined location seems far-fetched, Hosech (1937) observes that we readily accept the opposite behaviour in birds which lead potential predators *away* from their nests or chicks (e.g., Gochfeld 1984; Caro 2005; Gómez-Serrano and López-López 2016). Both behaviours require a sense of direction (where am I heading?) and a sense of position (where am I, relative to where I need to go?). As such, selection for the spatial cognition ability required by honeyguides to guide towards previously-located bees may have developed in a similar way to the defensive 'leading away' behaviour observed in sandgrouse, go-away birds and numerous shorebird species (Caro 2005; Gómez-Serrano and López-López 2016). Given the likely length of human-honeyguide interactions over evolutionary time (see above), there has likely been ample opportunity for humans to exerted selective pressure on honeyguide behaviour resulting in behaviour such as this, even though the human–honeyguide mutualism is non-obligate (neither species depends on it for survival) and honeyguides lack obvious morphological adaptations for cooperation. Adaptations such as the ability to learn local signals of cooperation (e.g., Isack 1987; Spottiswoode et al. 2016; Spottiswoode and Wood 2023) would likely have increased the mutual benefits gained from interacting by increasing the rate at which humans located bees' nests.

The biology of the greater honeyguide

The greater honeyguide (*Indicator indicator*) is one of 16 bird species in the family Indicatoridae, split into four genera: *Prodotiscus* (three species), *Melignomon* (two species), *Indicator* (ten species) and *Melichneutes* (one species) (Gill et al. 2023). All but two of these species are found on mainland Africa (Fry et al. 1988). Greater honeyguides are sexually dimorphic: adult females are a drab grey-brown with a dark bill (Figure 1.2), and in Niassa have a mass of 46.8 ± 5.6 g (mean ± Standard Deviation; SD), n = 39, range: 35–57 g (Cram et al. 2023) and have the same distinctive white outer tail feathers as males. Adult males tend to be slightly heavier than females. In Niassa, males have a mass of 48.8 ± 3.9 g (mean ± SD), n = 49, range: 36–58 g, and have a black throat patch, a distinctive pink bill (which tends to fade with age), pale ear coverts and small yellow 'epaulettes' on their upper shoulders (Figure 1.2).

Juvenile birds exhibit delayed plumage maturation, and after hatching until around 1 year have a bright yellow throat and breast and green-brown back (Fry et al. 1988). Until around 6 months old, juveniles often also have a light blue eye ring. At all ages greater honeyguides have thick skin thought to be a defence against bee stings (Short and Horne 2001) and are capable of guiding behaviour, except possibly when very young (Short and Horne 2001; Cram et al. 2023). In the wild, greater honeyguides have been recorded to live at least 7 years (unpublished data from Niassa).

Like other honeyguide species, greater honeyguides are obligate brood parasites, that lay their eggs in the nests of other hole-nesting bird species (Friedmann 1955). The young hatch with a distinctive bill hook (Friedmann 1955), used to kill the offspring of their foster parents (Spottiswoode and Koorevaar 2012). Greater honeyguide eggs are thick-shelled as a defence against puncturing by hosts (Spottiswoode and Colebrook-Robjent 2007) and broadly mimic their hosts' eggs in size and shape (Spottiswoode et al. 2011). Selection on egg dimensions appears to be imposed by competition among honeyguide females themselves (because of multiple females attempting to lay eggs in the same host nests), rather than by hosts (Spottiswoode 2013). Greater honeyguides parasitize numerous species, with hoopoe (*Upupa* spp.), wood-hoopoe (*Phoeniculus* and *Rhinopomastus* spp), kingfisher (*Halcyon* spp.) and bee-eaters (*Merops* spp.) generally the most common hosts (Fry et al. 1988; Spottiswoode and Colebrook-Robjent 2007).

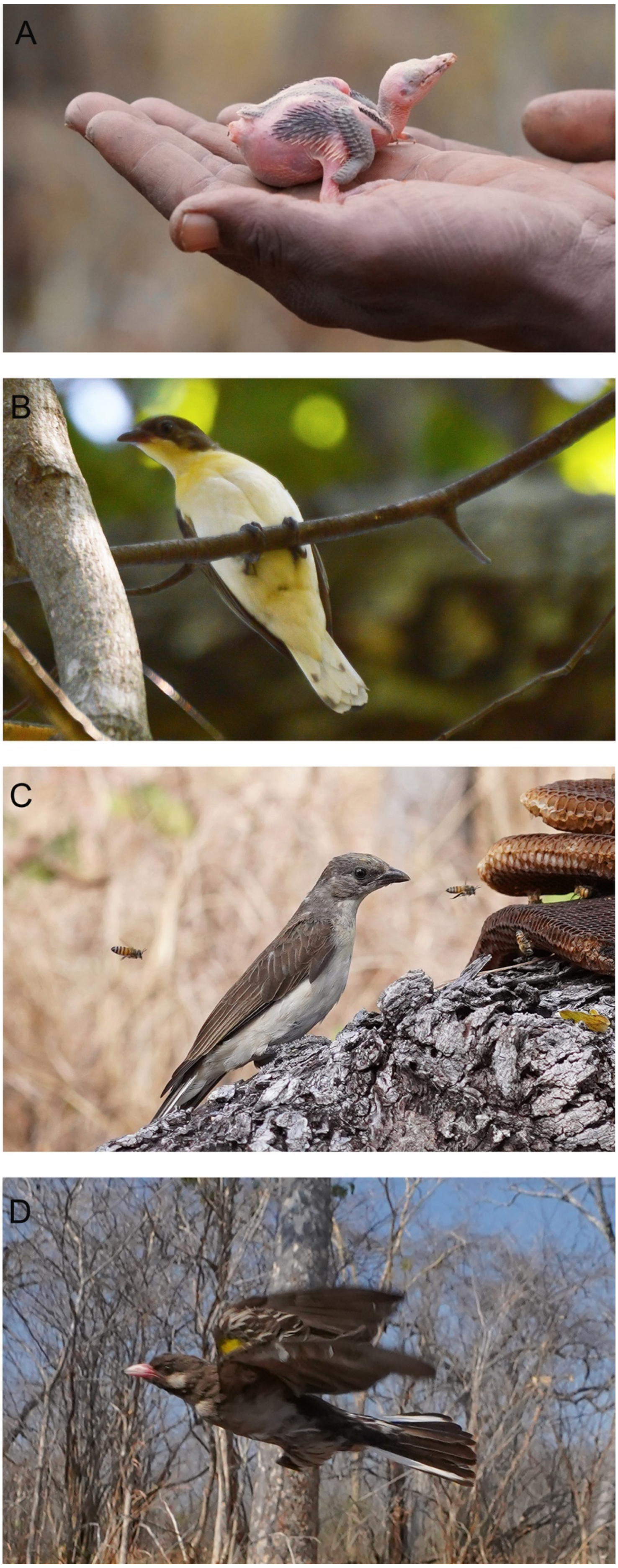
A
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Figure 1.2. (A) Greater honeyguide chick from Niassa temporarily removed from its little bee-eater (*Merops pusillus*) nest hole to take blood samples. (B) Juvenile greater honeyguide aged less than 6 months determined from its green-brown back and yellow throat and belly (sex unknown at this stage). (C) Adult female greater honeyguide near beeswax left by Yao honey-hunters after a harvest. (D) Adult male greater honeyguide in flight after being released from the hand following colour-ringing. The yellow upper-wing coverts, distinctive white outer tail feathers and pink bill are on display.

Within greater honeyguides are two highly divergent mitochondrial DNA lineages associated with ground- and tree- nesting hosts (Spottiswoode et al. 2011). Host-choice is inherited maternally, and birds in the 'tree-nesting' lineage are significantly heavier than those in the ground nesting lineage (Spottiswoode et al. 2011). Both lineages are present at Niassa (unpublished data). In recent work (Cram et al. 2023), we found that while greater honeyguides of all sizes guided in Niassa, birds with longer tarsi scrounged (rather than guided) more, and that the lightest females rarely guided, perhaps to avoid aggression over wax harvests or perhaps because these genetic matrilines affect body mass and behaviour. In the same study, the estimated density of honeyguides in the study area was 16.58 honeyguides per km^2, and we estimated that 23.7 ± 12.1 (mean ± SD) honeyguides are likely to hear a calling honey-hunter on an average-length honey-hunt.

The Niassa Special Reserve

All research conducted for this thesis was carried out over an area of 812 km^2 within Niassa Special Reserve, northern Mozambique (Figure 1.3). Further details about our collaboration with honey-hunters from Mbamba village (12°12'S, 38°01'E) and the specific ecology of our study area are detailed in the methods sections of Chapters 2, 3, 4 and 5. Here I provide a broader overview of the reserve and its regional context.

Niassa Special Reserve (until June 2020 known as 'Niassa National Reserve', and hereafter 'Niassa') is located in northern Mozambique, primarily within the Niassa Province. It is situated adjacent to the Ruvuma River and borders the United Republic of Tanzania along its northern boundary (Figure 1.3). Niassa covers an area of 42 300 km^2, accounting for 36% of protected area within Mozambique. It was officially established as a Game Reserve in 1954 and is divided into

17 management blocks (Allan et al. 2017). Eleven of these blocks are designated for sport hunting and six for biodiversity conservation and/or ecotourism (NCP 2022; Jorge et al. 2013).

One of the most striking features of Niassa is its management as a multiple land use area, with a resident population of ca. 67,000 people of the Yao, Matambwe and Macua cultural groups living across 45 villages and the towns of Mecula and Mavago (National Institute of Statistics 2017). The local population primarily depends on farming, fishing, honey-hunting, and employment in hunting or conservation managed blocks to sustain their livelihoods (Cunliffe et al. 2009; Jorge et al. 2013; Lubega et al. 2021). Previous surveys show that up to 91% of households participate in collecting, producing, and selling non-timber forest products (Lubega et al. 2021).

Northern Mozambique is renowned for its honey and beeswax production as far back as the 1500s (Popplewell and Harcus 1938; Colson and Cluckman 1959; Anstey 2009). Niassa is also one of relatively few areas in sub-Saharan Africa where cooperation with honeyguides is an active, routine, part of many peoples' daily lives. The conditions in which the human-honeyguide mutualism currently functions are likely to be similar to those under which the mutualism evolved (see Cram et al. 2023; Lloyd-Jones et al. 2022; Spottiswoode et al. 2016). Residents of Niassa depend substantially more on wild honey compared to beehive-produced honey. Some traditional beekeeping using bark hives has reportedly been present in the reserve for a long time (Ribeiro et al. 2019), although I did not observe any bark hives during fieldwork. Some beekeeping using modern top-bar hives takes place around human settlements, but these have not been present for more than 15 years and were not introduced specifically as an alternative to honey-hunting.

Ecologically, Niassa contains one of the largest protected areas of Miombo woodland in Africa (Timberlake et al. 2003) and is comprised primarily of deciduous, broad-leafed woodlands. The Lugenda river runs 300 km through the reserve and meets the Ruvuma river in the north-eastern corner at an elevation of 150 m. Topographically the reserve is higher in the west (ca. 1370 m elevation) and falls as an undulating plateau to 300–600 m elevation in the east. The central and eastern areas of the reserve are interspersed with distinctive granite inselbergs jutting out of the plain up to 600–900 m elevation (Figure 1.3). The overall climate is tropical, and temperatures range from 20–30°C in the dry season (May–November) and 25–40°C in the wet season (November–April). Rainfall begins in November and ends in late April or early May; during this period precipitation averages 250–350 mm per month (Timberlake et al. 2003).

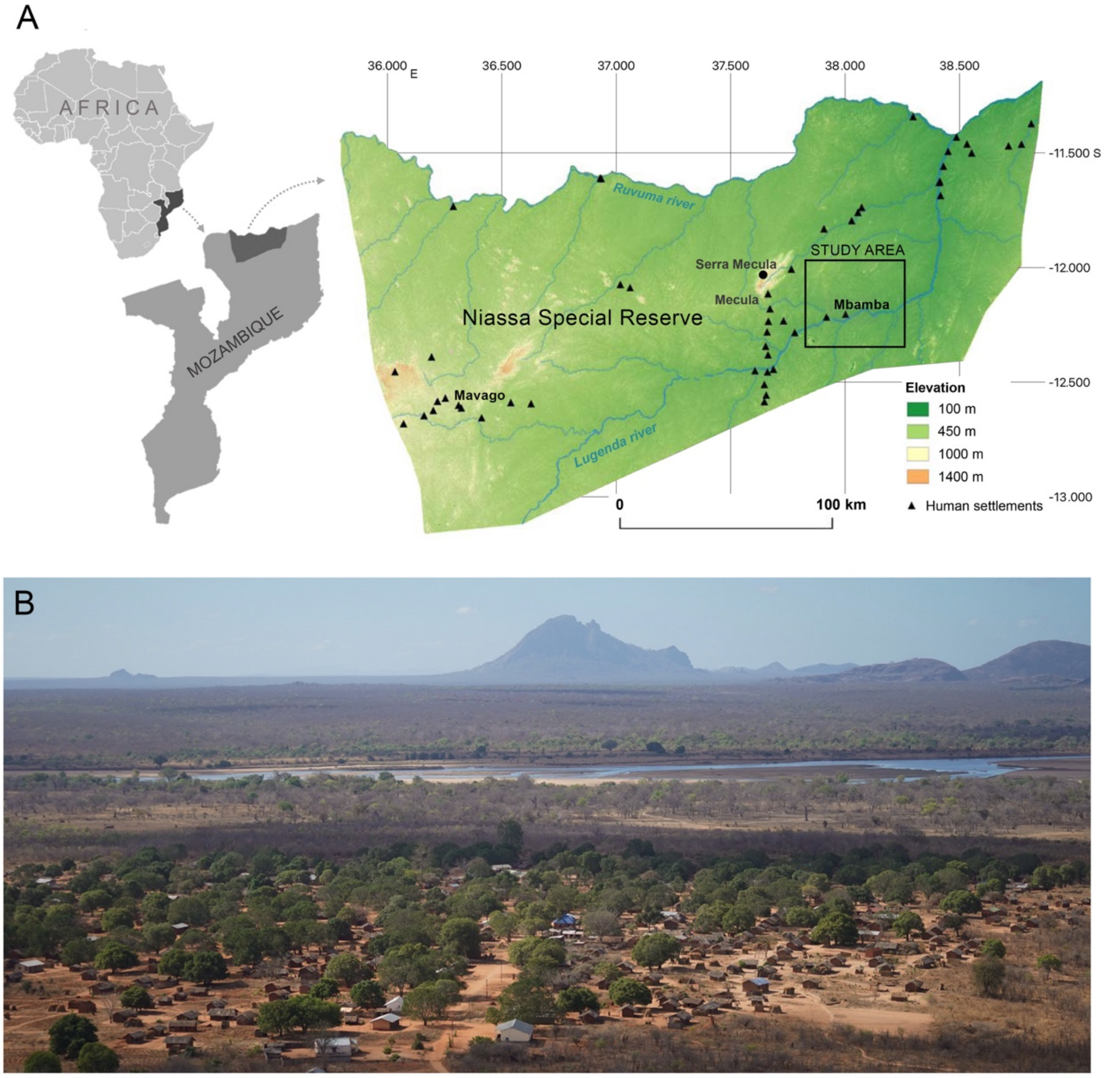


Figure 1.3. (A) Geographical context of Niassa Special Reserve with major rivers and the primary study area marked. (B) Aerial photo of Mbamba village, home to ca. 2000 inhabitants and central foraging location for > 30 regular 'professional' honey-hunters.

Thesis aims and structure

The objective of this research is to better understand the ecology and evolution of the honeyguide-human mutualism and specifically gain insights into: (1) the benefits of participating in the mutualism relative to non-participation, (2) the costs of cooperation and the consequences of non-cooperation, (3) how ecological context and wax-eating competitors impact the mutualism, and (4) how the mutualism impacts the local ecological community via tree-cutting. The findings presented here benefit from having humans as both contributors and participants in this unique mutualism. This unusual situation enables human honey-hunters to act as both mutualists and data-collectors, whose motives, decisions, energetic investment, and rewards can be investigated.

In this thesis I address the above questions in four data chapters, as follows:

CHAPTER 2 presents data on the behaviour of greater honeyguides, with a particular focus on the specific behaviours required by bird and human to be successful cooperators (Figure 1.4). In this chapter, I evaluate I whether honeyguides: 1) are found in any part of a landscape with wild bees' nests, 2) directly guide humans to bees' nests, 3) successfully show humans bees' nests more often than they fail, 4) significantly increase the rate at which bees' nests are found compared to bees' nests that humans find on their own, 5) guide to multiple bees' nests if the first one is not harvested, and 6) guide humans to bees' nests in trees amenable to harvest. I also investigate asymmetry in the rewards gained from mutualism, and potential conflicts of interest arising. I use several types of data, particularly a large, multi-year dataset of human-honeyguide interactions (collected from 2017–2022) to quantify the costs and benefits of successful and failed interactions for honeyguides and humans, and assess their implications for the mutualism's persistence.

CHAPTER 3 presents data on the influence (and exploitation) of the mutualism by other honeyguides and heterospecific species (Figure 1.4). I focus on understanding whether bird and mammalian wax-eating competitors threaten or stabilize the mutualism. This chapter uses data collected using camera traps set up to monitor feeding visits to wax made available following honey harvests. This chapter has been published in *Proceedings of the Royal Society B: Biological Sciences* (Lloyd-Jones et al. 2022).

CHAPTER 4 presents data on a rare behaviour within the mutualism for which one interpretation is punishment (a behaviour rarely observed in nature; Jensen 2010; Raihani and

Bshary 2019; Raihani et al. 2012). Like for many mutualisms, the partners in the human-honeyguide mutualism sometimes fail to reciprocate their partner for cooperation. Humans may fail to harvest the nest or reward the bird, and the guiding honeyguide sometimes fails to show a human a bees' nest (Spottiswoode et al. 2016; Wood et al. 2014). Is guiding to non-bee animals a response to non-rewarding by humans, or are there better supported hypotheses? In this chapter I use a range of field data, including acoustic, movement and behavioural responses to evaluate the evidence for a punishment hypothesis and four alternative hypotheses, with the aim of better understanding whether uncommon or rare behaviours such as guiding to non-bee animals are either adaptive or aberrant. This chapter has been accepted for publication, pending minor revisions, in *Ecology and Evolution*.

CHAPTER 5 presents data on the broader effects of the mutualism on the ecosystem (Figure 1.4). In this chapter, I investigate tree selection by bees in the woodland around Mbamba village, Niassa Special Reserve, and the effects of tree cutting due to honey-hunting activity. I present data on the species, size and harvest rates of trees containing bees collected over six years (2017–2022) from an area measuring 627 km^2. I also evaluate the specific influence of honeyguides on which trees get cut down for honey-harvests and quantify the landscape-level effects of honey-hunting.

CHAPTER 6 contains a synthesis and discussion. All references cited throughout are listed following Chapter 6. Appendices corresponding to Chapters 2, 3, 4, and 5 are included after References, arranged sequentially. All the data chapters have either been published, accepted for publication, or prepared with future publication in mind, resulting in some inevitable repetition in the introduction and methodology sections.

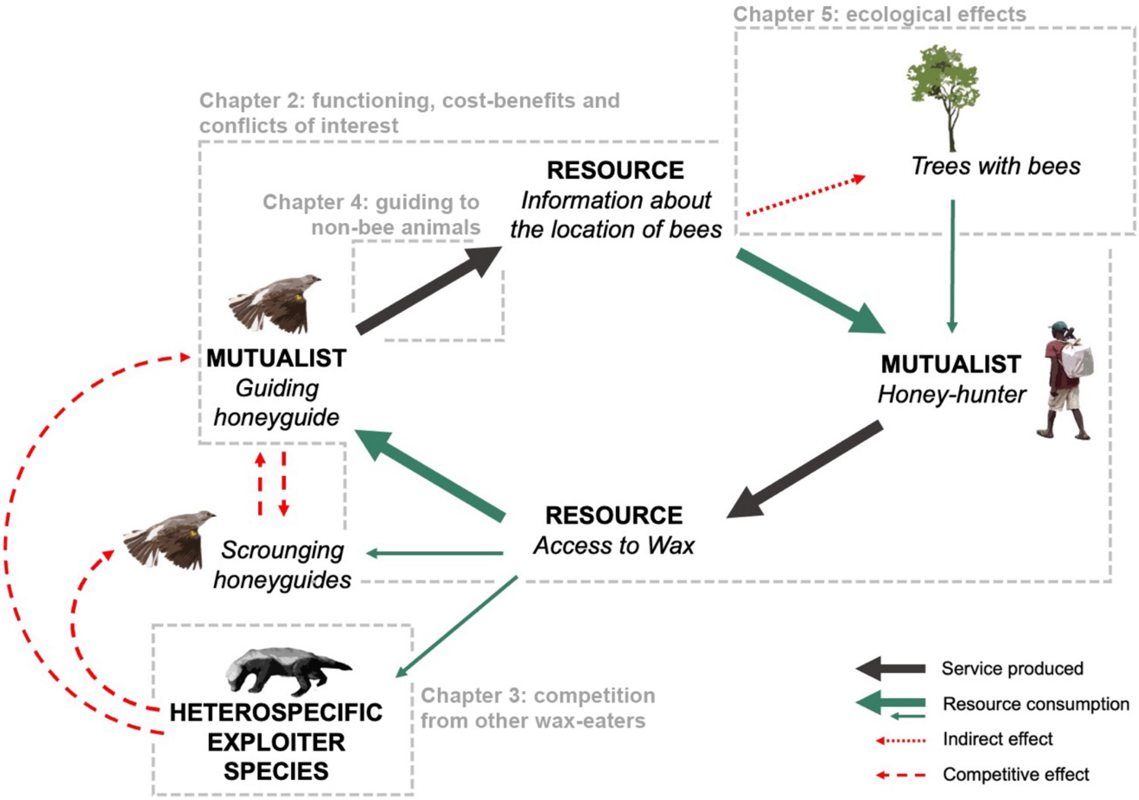


Figure 1.4. The human-honeyguide mutualism represented as a consumer-resource diagram with the areas of focus for each of the data chapters highlighted by grey dashed lines. Consumer-resource diagrams such as this emphasize resource flow rather than net effects, which aid in understanding the influence of competition on the mutualism (Jones et al. 2012). The black arrows represent the production of a resource (or service provided), the green arrows represent the consumption of a resource, dashed arrows represent a competitive or negative effect and the dotted arrow an indirect effect. The thickness of the solid arrows are approximations of the relative strength of resource flow.

CHAPTER 2

How to be a honeyguide: costs and benefits in a human-bird mutualism

Abstract

In a rare and likely ancient example of vertebrate-vertebrate mutualism, greater honeyguides (*Indicator indicator*) guide humans to wild bees' nests in Africa. Humans gain information about the location of bees' nests from which to harvest honey, while honeyguides gain access to beeswax which they eat. This relationship offers a particularly tractable system in which to study mutualism, since our own species is half the partnership. In this chapter I used a long-term dataset on honeyguide-human interactions in this system, primarily collected by a group of honey-hunters in northern Mozambique, to quantify mutualistic investment and rewards, and conflicts of interest between partners in this mutualism. I first characterize in detail how honeyguide-human cooperation functions in the ecological and cultural setting of northern Mozambique. I use data from 1,474 separate human-honeyguide interactions to quantify where, when and how much honeyguides help humans. I find that honeyguides: (1) are found in any part of a landscape with wild bees; (2) directly guide humans to bees' nests, demonstrating that they know where bees' nests are located; (3) successfully guide humans to bees' nests more often than they fail; (4) significantly increase the rate at which bees' nests are found and reduce the

search distance per bees' nest, compared to bees' nests that humans find on their own; (5) can guide to multiple bees' nests if the first one is not harvested; and (6) more often than not, guide humans to bees' nests in trees amenable to harvest. Second, I investigated a hypothesis of asymmetry between the honey and beeswax rewards gained by each partner, and a resultant conflict of interest. I found asymmetry in rewards gained by each partner, but that cooperation between honeyguides and humans nonetheless succeed (i.e., both partners gain a reward) more often than it fails. This high proportion of successful cooperative interactions, together with the low costs of failed interactions, together contribute to the persistence of the mutualism.

Introduction

Mutualisms are a fundamental form of ecological relationship in which two or more species receive reciprocal benefits, and underpin biodiversity, ecosystem functioning and nutrient cycling across the globe (Klein et al. 2007; Bronstein 2015). Mutualistic relationships range from plant–bacterial mutualisms, which generate an estimated 60% of annual terrestrial nitrogen input (Zahran 1999), to terrestrial ant-plant mutualisms (Palmer 2008, Kamaru et al. 2024) and marine coral-algal mutualisms (Mogen and Folke 1999). Studies across a wide range of empirical and theoretical mutualistic systems have sought to understand the persistence and stability of mutualisms despite competition from third-party species (Johnson and Bronstein 2019; Jones et al. 2012) and despite wide variation in the costs and benefits arising from 'mutual helping' behaviour between unrelated individuals (Ferriere et al. 2002, Herre and West 1997; Herre et al. 1999; Bshary et al. 2016).

In the study of mutualism, positive pseudo-reciprocal behaviours are those which require an initial investment enabling a recipient to perform a self-serving act, which in turn benefits the investor as a by-product (Bshary and Bergmüller 2008). Various authors have hypothesized that pseudo-reciprocal helping behaviour should be abundant in nature (Clutton-Brock 2009; Leimar and Hammerstein 2010) and that mutualisms should be stable at high densities of mutualistic partners (Hale et al. 2021; Morris et al. 2010). In game-theoretic models, stable mutual helping behaviour most commonly occurs in situations where each individual performs self-serving acts that benefit a partner as a by-product (Bshary et al. 2016). An example of a pseudo-reciprocal mutualism occurs between arbuscular-mycorrhizal fungi and plant root systems: a fungus, *Glomus intraradices,* provides more phosphate to plant roots which provide it more carbon, and in return, the root system of a plant, *Medicago truncatulus*, provides more carbon (sugars) to fungi that provide more phosphate (Kiers et al. 2011).

One system offering a compelling lens through which to examine mutualistic pseudo-reciprocity is found in Africa, between greater honeyguide (*Indicator indicator*) birds and humans (Friedmann 1955; Isack and Reyer 1989). Honeyguides innately possess the ability to locate wild bees' nests (Short and Horne 2001) and energy-rich beeswax complements their otherwise insectivorous diet (Diamond 1988; Chapter 2; Cram et al. 2023). To guide humans to bees' nests, honeyguides across Africa give distinctive chattering calls which attract the attention of honey-hunters (Friedman 1955; Isack 1987; Wood et al. 2014; Spottiswoode et al. 2016). Honeyguides then continuously produce such calls while indicating the direction to a bees' nest by flying from tree to tree (Isack 1989). Honeyguides may either spontaneously approach humans and attempt to guide them (Isack 1987; Short and Horne 2001), or can be attracted using culturally-maintained signals of cooperation that humans in some cultures specifically produce to increase their chances of being guided (e.g. Isack and Reyer 1989; Spottiswoode et al. 2016; Spottiswoode and Wood 2023).

After being guided to a bees' nest, a human honey-hunter decides whether or not to harvest the nest, typically using axes and smoke (Chapter 3; Spottiswoode et al. 2016). Following a harvest, in some human cultures people leave behind empty pieces of honeycomb as a reward for the honeyguide (Chapter 3), which the nearby waiting honeyguide later silently descends to and eats (Friedmann 1955; Isack 1987; Short and Horne 2001). In this way, honeyguides exchange information about the location of bees' nests, for access to beeswax food. This interspecies relationship is non-obligate, as honeyguides appear to be able to survive without wax in their diet (Fry et al. 1988; Diamond and Place 1988) and sometimes to gain access to wax without humans (Isack 1987), and humans can, at times, find honey without the cooperation of honeyguides (Isack 1987; Wood et al. 2014; Spottiswoode et al. 2016; this chapter). Guiding behaviour is, however, likely to have been an important selective force in honeyguides' evolutionary history (Sachs et al. 2004), since honeyguides possess specialised adaptations (innate attraction to humans, production of the specialised guiding call, and guiding behaviour) that aid cooperative success.

Humans are unable to coerce honeyguides into guiding them to bees, or vice-versa. This means that the human-honeyguide partnership is characterized by flexible individual decision-making. This flexibility provides an opportunity to observe how mutualistic interactions are initiated and maintained in response to the strategic behaviours of the participants and the spatial distribution of resources (Jones et al. 2015). Furthermore, selective pressures that shape organisms to maximize individual fitness and resolve conflicts of interest in their favour could be expected to arise whenever non-relatives interact (Sachs and Simms 2006). Understanding how mutualisms persist despite conflicts of interest is important because the possibly is ever-present that each partner may benefit from either overexploiting or abandoning their partner (Ferriere et al. 2002; Sachs and Simms 2006).

Yao honey-hunters have a cultural tradition of leaving behind a small pile of wax for honeyguides following a harvest. Honeyguides do not necessarily need this active form of reward to access wax (Chapter 3) and guiding a human to any harvestable bees' nest should be sufficient to gain a reward if the bees' nest is harvested, since small wax scraps nonetheless provide a relatively large food reward to a small bird (Table 2.1). By contrast, for a human, only a harvestable bees' nest with a substantial quantity of honey is enough for the benefit to exceed the energetic cost of harvesting (Table 2.1). As expected from optimal foraging principles, humans seek to gain the largest quantity of honey possible, while minimizing the energy used to locate and harvesting bees' nests (Wood et al. 2014; Marlowe et al. 2014). Bees' nests vary greatly in profitability to a human, since some nests are costly or impossible to harvest (due to e.g., tree size and wood hardness; see Chapter 5). Some bees' nests may also contain little honey due to colony age or season. There is therefore a possible asymmetry between these mutualists in what constitutes a profitable bees' nest: for a honeyguide, the selective imperative is simply for a harvest to occur, whereas for humans, the selective imperative is a harvest of a bees' nest where the benefits outweigh the cost.

The resource benefits (honey and wax) gained from the honeyguide-human system are readily measured and can be linked to the energetic investments made by humans. Quantifying these economic values is a crucial step in any ecological or evolutionary study of a mutualism (Bergstrom et al. 2003) and can be particularly important for a consumer-resource mutualism such as this (Holland and DeAngelis 2001; Jones et al. 2012). For this research, a custom method was developed to record numerous human-honeyguide interactions in a landscape across space and over time. Twenty-one honey-hunters living in Mbamba village, Niassa Special Reserve, northern Mozambique, recorded honey-hunting effort and payoffs from their interactions with honeyguides from 2017 to 2022. These data included GPS tracks of their honey-hunting trips, the incidence and duration of guiding interactions, rates of success, measurements of the trees containing a bees' nest, honey-hunters' decisions of whether or not to harvest a bees' nest, resource payoffs to the humans (mass of combs containing honey and brood taken by honey-hunters) and to the honeyguide (whether or not a nest was harvested, and mass of empty wax combs or combs containing brood left behind).

In section one of this chapter, I build on past studies (e.g., Friedmann 1955; Isack 1987; Wood et al. 2014; Spottiswoode et al. 2016) by describing in spatial and temporal detail the 'how' of human-honeyguide cooperative interactions in Niassa. I evaluate six attributes and behaviours of honeyguides which contribute to successful mutualism with humans. Specifically, whether honeyguides (1) are found in any part of a landscape with wild bees' nests; (2) directly guide humans to bees' nests and know where bees' nests are located; (3) successfully guide humans to bees' nests more often than they fail; (4) significantly increase the rate at which bees' nests are found and reduce the search distance per bees' nest, compared to bees' nests that humans find on their own; (5) guide to multiple bees' nests if the first one is not harvested; and (6) guide humans to bees' nests in trees amenable to harvest.

In the second section of this chapter, I evaluate a hypothesis relating to asymmetry in the rewards of honey and beeswax gained by each partner, and whether asymmetry causes a conflict of interest between the partners over what comprises a profitable bees' nest to guide or be guided to. There are four ways in which an interaction between a honeyguide and human can end, and each scenario has different repercussions on the benefits gained by each party (Table 2.1). Because of the vast difference in size between honeyguides and humans and so the respective energy needed for benefits to outweigh costs, I hypothesize that the rewards of this mutualism are asymmetrical. This hypothesis predicts that the benefits gained from harvests should be less variable for honeyguides than for humans. If there were a conflict of interests, then there should be more honey-harvests from which the honeyguide gains and human does not (+ honeyguide, – humans in Table 2.1) compared to those from which a human gains and the honeyguides does not (– honeyguide, + human) in Table 2.1).

Together, the descriptive and hypothesis-driven sections of this chapter seek to provide insights into the maintenance and stability of the human-honeyguide mutualism through a cost-benefit lens. This perspective allows us to quantify the costs of failed interactions for honeyguides and humans, and so to understand why failed interactions have not undermined the mutualism's persistence.

Table 2.1. Outcomes from human-honeyguide cooperative interactions, and whether for each partner this outcome is positive (+) or negative (–) in terms of a reward gained.

		Honeyguide	
		–	+
Human	–	Bees' nest is *not* found by human, human gains no information about location of a bees' nest, honeyguide gains no wax	Bees' nest is found by human, human harvests the nest but gains no honey, honeyguide gains access to wax
	+	Bees' nest is found by human, human chooses not to harvest the nest but gains information for possible later use, the honeyguide fails to immediately gain access to wax (but may also do so later yet without the same early-arrival advantage; see Chapter 3)*	Bees' nest is found by human, human harvests the nest and gains a honey reward, honeyguide gains access to wax

* This quadrant is least clear-cut, because the human benefit may also be zero if the nest is unharvestable or never harvested, and the bird benefit can be non-zero if it receives a future benefit from a harvest.

Methods

Study area

This study was carried out over an area of 812 km^2 within Niassa Special Reserve, northern Mozambique. The study area is defined by the range of Yao honey-hunters' foraging trips, radiating outwards from Mbamba village (12°12'0S, 38°01'0E) which has ca 2,000 inhabitants including > 30 regular honey-hunters. Niassa Special Reserve (hereafter 'Niassa') is 42,300 km^2 in size, managed as multiple land-use area, and contains some of the largest tracts of continuous miombo woodland in Africa (Timberlake et al. 2003; Ribero et al. 2017; Figure 2.1). Niassa has a human population of ca. 67,000 people of the Yao, Matambwe and Macua cultural groups who live across 47 villages (National Institute of Statistics, 2017). Inhabitants of Niassa primarily depend on farming, fishing and honey-hunting to sustain their livelihoods (Cunliffe et al. 2009; Lubega et al. 2021) and the reserve is one of the few locations in Africa where the honeyguide-human mutualism continues to thrive in an active form, as a routine part of many peoples' daily lives (Spottiswoode et al. 2016; Cram et al. 2022; van der Wal, in revision; this Chapter). People typically honey-hunt in small groups of 2–5 people, on trips undertaken on foot, either as day trips from the village or from temporary fishing or agricultural encampments, or as multi-days trips involving camping out for 2–4 nights. Honey is both used for personal consumption and sold at local markets.

The study area has an elevation of 380–450 m above sea level and the climate is sub-humid tropical, with mean minimum and maximum air temperatures ranging between 16–33°C in the dry season (May–October) and 22–32°C in the wet season (November–April) (Timberlake et al. 2004). Honey-hunting and bee data were collected in miombo or riverine habitat, often near or along the Lugenda, Msanjesi, Mbamba and Mpopo rivers where tree diversity can be distinct from the miombo habitat (Chapter 5). Rainfall begins in November and ends in late April or early May, and during this period precipitation averages 250–350 mm per month (Timberlake et al. 2004). Bees' honey stores build up throughout the rains with the flowering of dominant species and peak in May–June, then deplete as the dry season progresses, and then peak again in November–December following the flowering of trees prior to the following rainy season, in common with other parts of Africa where seasonality is primarily determined by rainfall (Lawton, 1982).

Data collection

Two datasets were used in this chapter, described in detail below: (1) *Honey-hunter collected data*: this consists of foraging GPS movement data, records of honeyguide interactions and of data on 3,317 trees containing bees' nests, collected by 21 Yao honey-hunters from Mbamba village using a custom application loaded on ruggedized smartphones, between June 2017 and September 2022. This was used to measure the attributes and behaviours of honeyguides contributing to successful mutualism with humans. (2) *Audio recordings of human signals to honeyguides*: this consists of a set of 41 audio and GPS-recorded guiding interactions made from 6 to 27 June 2018. It was used to calculate rates of vocalization by humans directed towards honeyguides whilst searching for honeyguides, and while following honeyguides, prior to either finding a bees' nest or the interaction failing (dataset overlaps with that used in Chapter 4). In addition, I report qualitative observations personally made on > 205 days of honey-hunting and > 300 first-hand experiences of being guided to bees' nests whilst accompanying Yao honey-hunters, and from three instances of being guided alone by a honeyguide to a bees' nest in Niassa, between 2017 and 2023.

Honey-hunter collected data. Along with Claire Spottiswoode I set up a custom data collection system to allow a group of honey-hunters to self-collect a variety of data about their honey-hunting activities, interactions with honeyguides and the trees which they were guided to. Between 14 and 21 active honey-hunters (19 men and two women) collected data between 2017 and 2022, and all were selected for involvement in this study based on guidance from the traditional chiefs of Mbamba village and as well as direct honey-hunting experience with them. Our icon-driven application (designed by myself, Andrew Rayner of HabitatInfo, Wales, UK, and Claire Spottiswoode) contains a series of steps mimicking the natural progression of a honey-hunt with a range of possible outcomes (e.g., the icons for the following questions could occur in this sequence: "Were you guided by a honeyguide?" [yes], "What happened next? [found tree], "Did you harvest the honey?" [yes], "Did you cut the tree down?" [yes], "How much honey did you take?" [mass in kg]). See Appendix to Chapter 2 for a diagram with all possible decisions. The icon-driven interface, also contained a few widely understood Kiswahili words as prompts, which proved to be highly compatible with low literacy rates. The app was loaded and run on rugged handheld Android devices (Cedar CT5, Juniper Systems, Logan, Utah, USA) featuring accurate GPS capabilities.

Whilst collecting data with the application, honey-hunters recorded all significant honey-hunting 'events' occurring during each 'trip' away from the village, and all 'event' inputs were stored with corresponding GPS coordinates and time of day. During use, the input of a response at any step moved the user on to a page with a number of logical following steps, but if an input error was made, the user was also able go back to the previous step using the 'back button'. All such 'back button' presses were also recorded as individual 'events', greatly assisting with reviews of data accuracy. Whist recording the identification of trees and photographing bees' nests, the application required an image of the bees' nest, tree and a voice note to be recorded. These five-second voice notes allowed the user to vocally identify the tree species in either Yao or Macua, and these voice notes were compared to corresponding images of trees for verification of input data accuracy. All voice notes were manually transcribed by myself, Orlando Ncuela and Rachel Lloyd-Jones. Honey-hunters were paid a fixed monthly stipend of 1,200 Mozambican Meticals (in 2017, increasing to 2,000 by September 2022) to compensate for the extra time taken entering data. The value of the stipend was carefully considered to strike a balance between compensating the honey-hunters for the time taken to record data and to take care of the recording equipment, while also not incentivizing additional honey-hunting activity by greatly shifting the cost-benefit balance of their activities. Data-collecting honey-hunters were paid for all months of the year regardless of the quantity of data they collected, to avoid incentivizing greater than normal activity.

Data from the application were saved in SQL database form and copied from the devices periodically (initially monthly, later twice a year). All data were reviewed in R (R Core Team, 2023), primarily using a custom R shiny application developed by Brian M. Wood (Appendix to Chapter 2). This interface mapped events and images spatially alongside tabular data, and after the review of each event or trip, integrated the reviews back into the SQL database. Events were reviewed in a consistent way using a set of rules to remove unintentional records, training trips and other inconsistencies. Data reviews were undertaken by myself, Tom Bachmann and Rion Cuthill.

Honeyguide and human audio recordings. Between 6 June 2018 and 27 June 2018, I made 41 recordings while accompanying two Yao honey-hunters (different combination of 10 people) as they elicited guiding behaviour from honeyguides and followed honeyguides in a natural setting. Foraging trips made to record honey-hunters began along vehicle tracks at intervals at least 500 m apart, and at least 1,500 m apart when conducted on the same day, to reduce any confounding effect of prior interactions with honeyguides. In all other ways these trips resembled natural honey-hunting excursions and were as uninfluenced by the observer and recording activity as possible.

Instructions were given to the two honey-hunters to vocalize and interact with honeyguides in whatever way they normally would whilst honey-hunting, and to walk, stop or search trees at any speed or in any manner they saw fit. Honey-hunter vocalizations were recorded in WAV format using a lavalier microphone (AudioTechnica, Tokyo, Japan) attached to their shirt collars connected to a Tascam DR-05X recorder (TEAC Inc., CA, USA). These audio recordings began prior to guiding and continued until bees were located, or once the honey-hunters determined that the honeyguide had failed (i.e., went quiet). All call types (Figure 2.1D) were manually categorized by either myself or Orlando Ncuela, who listened to and manually recorded the timestamps for each vocalization.

Permits. Data collection was carried out with full informed consent and received approval from the University of Cape Town Faculty of Science Research Ethics committee (approval numbers FSREC 22–2017 and FSREC 50 - 2018), Administração Nacional das Áreas de Conservação, and the Traditional Chiefs of Mbamba Village.

Statistical analyses

All statistical and spatial analyses were conducted using R version 4.3.0 (R Core Team, 2024). I first summarised the percentage of honey-hunting trips originating from: (1) Mbamba village (defined as a 0.49 km^2 polygon covering all village dwellings) or (2) fishing and agricultural camps, or were (3) multi-day trips classified based on the point of origin (respectively within the village, along the river at known fishing camps, within fields around the village, or >10 km from the village). When data were collected by more than one individual in a honey-hunting party, each trip was only counted once, selected on a metric of data quality (usually based on the smallest number of missing data points if mistakes were made during collection, or if all equal, then first in the list for that day).

The relationship between human-honeyguide interactions and distance from Mbamba village was calculated by counting the number of interactions found within 1 x 1 km raster grid cells laid across the study area. The relationship between these densities and distance from the village was tested using a Generalized Additive Model (GAM) with count as the response variable and distance as the predictor, with a Gaussian error distribution and identity link function using the *mgcv* package (Wood 2017). The relationship between bees' nests found (with and without following a honeyguide) and distance from Mbamba village was similarly calculated using the same 1 x 1 km gird cell raster. This relationship was also modelled using a GAM with bees' nest count as the response variable and distance as the predictor.

To test seasonality of honey-hunting, I visualized adjusted counts of cooperative interactions (these are true counts multiplied by an adjustment factor to account for a constantly varying numbers of data collectors) between honeyguides and humans over 6 years, yielding counts standardised to the maximum number of data collectors (n = 21). To test whether honey-hunting activity peaks at any point in the year, I used a circular statistics test for uniformity, Rao's Spacing Test (Rao 1972).

Encounter rates with honeyguides, and rates of finding bees' nests with and without honeyguides, were derived as follows below, from the following GPS data collected using the application whilst honey-hunting: (i) total track distances per day, (ii) distances between when a honeyguide first started guiding and when a bees' nest was found or the interaction failed, and (iii) 'commuting' distances between when honey-hunters selected the 'Leave home' icon in the application and when they first started soliciting cooperation (i.e., selected the 'first started honey- hunting' icon in the application). The rate of finding bees' nests without honeyguides was calculated as the number of bees' nests found without honeyguides divided by the sum of total distances covered, minus the sum of commuting distances and distance spent following honeyguides (following Wood et al. 2014 except for the subtraction of distance spent following honeyguides). The rate of finding bees' nests with honeyguides was calculated as the number of bees' nests found with a honeyguide's cooperation, divided by the total distance spent following honeyguides (regardless of whether the interaction was successful) (following Wood et al. 2014). Tracks which were incomplete or shorter than 1,000 m in a day were excluded (n = 303). The total human movement dataset includes 2,342 person-days (13,366 person-hours) of GPS-measured movement (178 person-days of female movement and 2164 person-days of male movement). From the total sample of 2,342 person-days, the application recorded track data for 5.7 ± 0.06 hours on average (mean ± SE) per person-day. Data cleaning was performed blind to the hypotheses of the study, but analyses were not performed blind to the hypotheses of the study.

To test for a difference in rates of finding bees' nests with and without honeyguides, I used a linear mixed-effects model (LMM). Rate of discovering bees' nests (number of bees' nests per hour averaged across all years for each honey-hunter individual) was the dependent variable, with guided or not guided as a fixed effect, and honey-hunter identity as a random effect. Data were analysed using the *lme4* package in R and the model was fitted using restricted maximum likelihood (REML), and significance assessed using Analysis of Variance (ANOVA). This was repeated to test for differences in distance covered per bees' nest found, with and without the cooperation of a honeyguide. Distance per bees' nest found was the dependent variable with guided or not guided as a fixed effect, and honey-hunter identity as a random effect.

To test for a relationship between the number of successful human-honeyguide interactions and the cumulative amount of honey gained per day, I first summarised the number of successful interactions per day, per honey-hunter, and removed replicate records (where two honey-hunters together recorded the same number of interactions). I then summarised all honey harvests, per honey-hunter per day. Due to overdispersion in the count data, I then ran a quasi-Poisson regression with number of guiding events per day as the response variable and amount of honey gained as the predictor.

To test whether humans were more likely to harvest bees' nests that they had been guided to by honeyguides compared to than bees' nests they had found by themselves, I used a Chi-squared test between the proportion of trees that humans choose to harvest when found with (n

= 1061) and without (n = 1642) the cooperation of honeyguides. For this analysis I excluded all baobab trees (*Adansonia digitata*) (n = 562 records, including many repeat visits of the same tree in different months or years) which, due to their size, are never cut down and rarely harvested. At least 108 separate baobab trees containing bees' nests were recorded. These are typically occupied by bees long-term and are well-known to many honey-hunters, and so easily found without the cooperation of honeyguides. However, including baobabs did not change the results of the Chi-squared test.

To test whether more honey was gained from harvests of bees' nests guided to by a honeyguide versus bees' nests found by the honey-hunters by themselves, I used a Generalized Linear Mixed Model (GLMM) with a Gamma distribution and a log link function. Mass of honey was the response variable, with the following fixed effects: a binary value indicating whether the bees' nest had been shown by a honeyguide or not, tree diameter at breast height (to account for its relationship between the mass of honey harvested), and honey-hunter ID as a random effect (to account for variability in honey obtained between people). This analysis used a dataset of n = 1,088 honey-harvests. I also tested whether more wax was left behind for honeyguides by honey-hunters at bees' nests they were guided to versus bees' nests they found by themselves, using the same model structure as for honey but with mass of wax as the response variable. This analysis was performed using a dataset of n = 968 observations collected by 21 honey-hunters (if values were not recorded at a realistic location, e.g., more than 500 m from a harvest, then they were excluded from this analysis. Inputting the mass of wax left behind was one of the last questions after a harvest and data collectors sometimes forgot to input data).

To test the hypothesis that the honey and wax rewards of this mutualism are asymmetrical, I first tested whether the benefits gained from harvests were less variable for honeyguides than for humans, using the *boot* package in R for bootstrap resampling (1000 replicates). This generates estimates of the difference in the standard deviations for measurements of honey and wax at each harvest and is a non-parametric approach robust for the assessment of variability differences (Efron and Tibshirani 1993). Non-overlapping estimates indicate a significant difference in variability. I tested whether honey and wax yields from n = 1171 harvests were correlated using a Spearman's rank correlation. A Shapiro-Wilk test and visual assessment of a scatterplot were first used to identify linearity and homoscedasticity. I found that both variables violated assumptions of normality.

Lastly, I made the assumption that the energetic costs for a human harvesting a bees' nest are greater than 0.5 kg of honey divided by the number of honey-hunters present (Wood et. al. 2014) and that for honeyguides the costs of guiding a human are greater than the calories in 5 g of wax. Given this assumption, I tested whether the proportion of harvests for which benefits exceeded costs was greater for honeyguides than for humans. To do this I set biologically relevant thresholds of 0.5 kg for honey and 0.005 kg for wax, as above, and then counted the number of honey harvests for which honeyguides gained a benefit but humans did not, and the number of harvests from which humans gained a benefit but honeyguides did not. I then used a mixed-effects logistic regression model to test for a difference between the two groups (implemented using R package *lme4*). The predictor variable was a binary indicator of group (1 = honey harvests where honeyguides gained a benefit but humans did not, and 0 = harvests from which humans gained a benefit but honeyguides did not) with honey-hunter ID included as random effect.

Modelling the 'quality' of trees with bees' nests

I derived a metric of tree 'quality' (from a honey-hunters' perspective) to compare the quality of bees' nests found with and without honeyguides. Considerable ecological variation exists in the trees containing bees' nests. Because trees vary in size, species (influencing how hard their wood is and how difficult it is to cut into or cut down when harvesting honey; Chapter 5), and height of the bees' nest entrance, it is possible to use these three variables to model whether a given tree containing a bees' nest is more desirable to a honey-hunter for harvesting.

The height of the bees' nest entrance was modelled as a binary variable (< 2 m or > 2 m above the ground). This is because in most cases, trees containing a bees' nest > 2 m above the ground are cut down when harvesting honey, since it is rare for there to be an easy way to climb and stand in the tree while harvesting honey. Therefore, we expect a step change at bees' nest height of around 2 m in the likelihood of a tree being cut down to harvest the honey, with no linear change thereafter. Data-collecting honey-hunters did not directly measure nest entrance height, so we manually classified whether or not the entrance was above or below 2 m above ground using photographs they took of all bees' nests. A subset of trees (4 %; 117 of 2,703) for which entrance height was uncertain was excluded from this analysis.

Conversations with Yao honey-hunters indicated that they believe that larger honey harvests are made further from the village where there has been less honey-hunting activity. To test whether distance to village predicts honey-hunters' decisions whether to harvest a bees' nest, I first calculated straight-line distance from each bees' nest to the nearest point of a polygon of Mbamba village. I then fitted a logistic regression model to the data with tree (harvested or not) as a binary response variable, and the predictor variables of tree species (a categorical variable of 58 species recorded containing bees' nests), tree diameter at breast height and distance to village (both continuous), and nest entrance height (binary; < 2 m or > 2 m) (Table 2.2). I used backwards stepwise selection to simplify the model by removing predictors based on the AIC (Akaike Information Criterion) (Akaike 1974) and found that all three variables contributed to improving the model, and that the full model was the best fit (Table 2.2). Removal of tree species or tree size from the model particularly contributed to increased AIC values (Table 2.2). I then generated a continuous value of 'quality' for n = 2,703 trees based on this model (i.e., the predicted values from this model), and tested the relationship between distance to the village and this metric of quality for bee trees found with and without honeyguides, using a generalized additive model, GAM, with a binomial family and a logit link function.

Table 2.2. Ranking of models used to generate a 'quality' metric of all bees' nests found by Yao honey-hunters. The binary response variable 'harvest' indicates whether or not the honey-hunters chose to harvest the bees' nest.

Rank	**Model**	**Residual df**	**AIC**
1	harvest ~ tree species + tree dbh + bee entrance height	2719	3183.4
2	harvest ~ tree species + tree dbh	2721	3202.4
3	harvest ~ tree species + bee entrance height	2720	3221.5
4	harvest ~ tree dbh + bee entrance height	2777	3329.5

Results

Part 1: Human-honeyguide cooperation in Niassa

Locating honeyguides

Honey-hunting trips took three main forms. First, honey-hunters walked from the village on honey-hunting trips which lasted for less than a day and which were undertaken specifically to forage for honey (55.9 % of 2,342 trips). Second, honey-hunters foraged for honey for short periods starting out from fishing camps, or from small, cultivated 'shifting agriculture' farms (22.7 % of trips) surrounding the village, where during the crop growing season honey-hunters live in close proximity (< ~100 m) to habitat supporting bees and so also honeyguides. Such honey-hunting expeditions were often in the morning or the evening, and were reported in conversations to be primarily for the purpose of supplementing their diet that day with honey. Third, honey-hunters sometimes undertook multi-day honey-hunting trips from Mbamba (21.3 % of trips), where the first day involved walking a considerable distance (> 15 km) into an area regarded as ideal for honey-hunting, and which may be less visited by honey-hunters due to its distance from the village. Subsequent days on these multi-day trips, which lasted between 3–6 days overall, tended to loop back to a central campsite (Figure 2.2).

Any trips originating from Mbamba village required considerable energetic investment because relatively few guiding interactions between humans and honeyguides occur within 2 km (straight-line distance) of the village (Figure 2.2). This is because much of the immediate area around Mbamba has been cleared for shifting agriculture. Therefore, cooperative interactions tended to start occurring around 2 km from the village, increasing in density until around 5 km, and then flattened off, remaining consistent until the maximum distance (ca. 25 km) honey-hunters tend to travel from the village while honey-hunting (Figure 2.2). I found that the number of bees' nests found per square km, and number of honeyguide interactions, both peaked at 5 km from the village (Figure 2.2). The number of interactions and bees' nests recorded decreased as distance from the village increased, indicating a clear reduction in visits to such areas by honey-hunters. Very few honey-hunting trips (and interactions with honeyguides) extended beyond 20 km from Mbamba village (Figure 2.2).

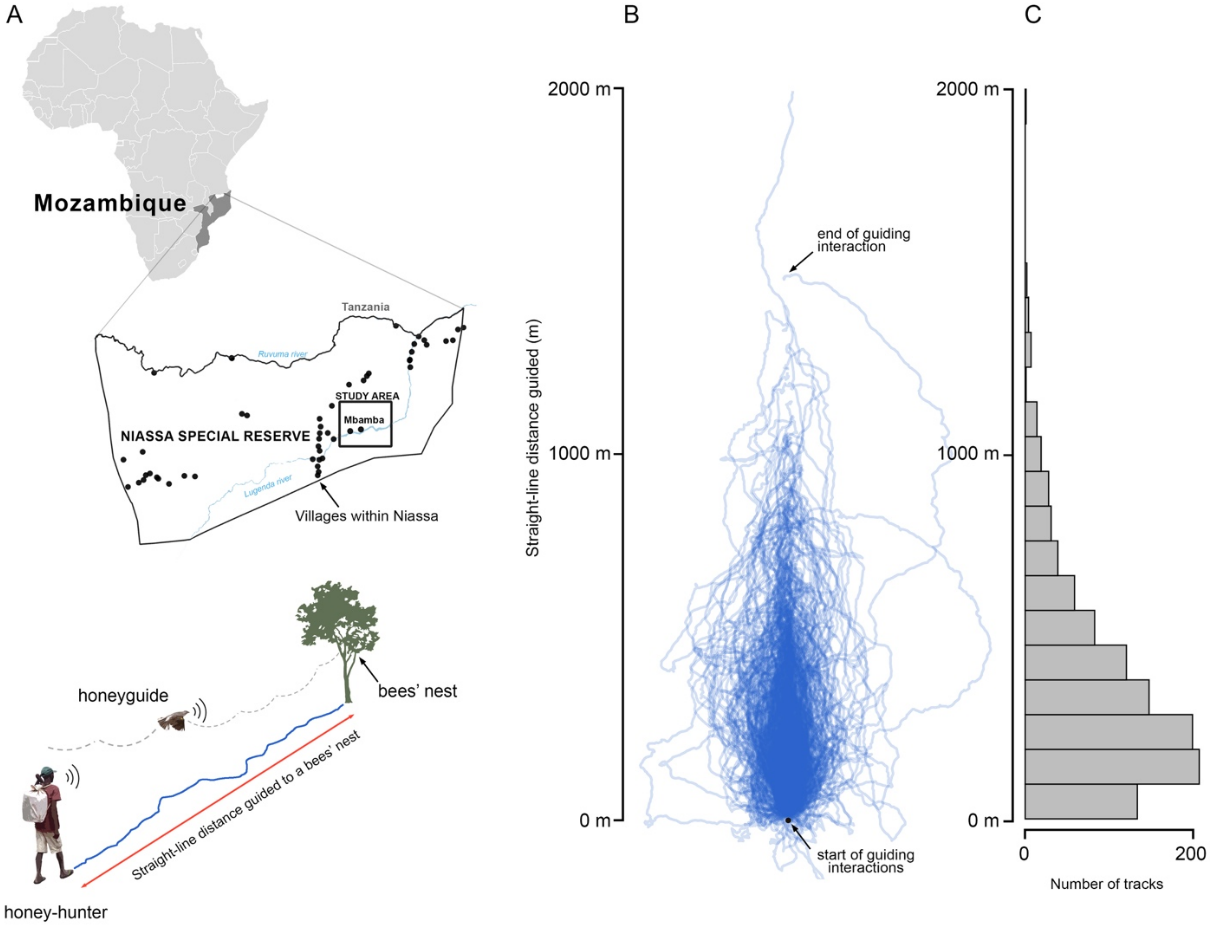


Figure 2.1. (A) Map of the study area in northern Mozambique and diagram of a honey-hunt. In this diagram, GPS-recorded tracks are represented as blue lines and straight-line distance as a red line. (B) The majority of guiding interactions are strikingly direct. In this figure, GPS tracks of guiding interactions are overlaid so that their starting points overlap and are rotated so that they all orient north-south. (C) Most guiding interactions cover a short distance (< 500 m), as shown by this frequency distribution of track lengths.

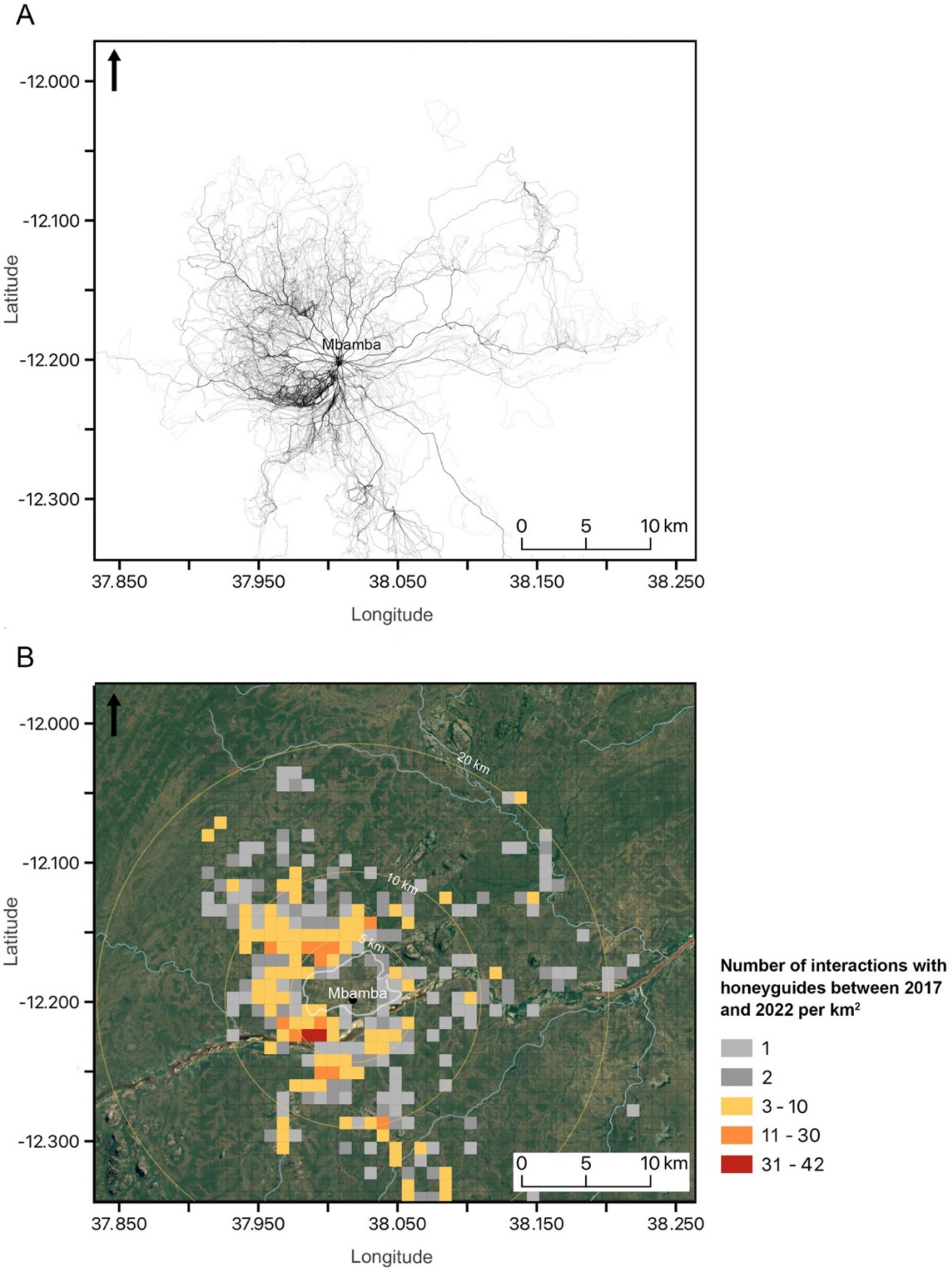


Figure 2.2. (A) GPS tracks of honey-hunting activity from and around Mbamba village, Niassa Special Reserve, and (B) number of guiding interactions found in 1 km^2 grid cells around Mbamba village, recorded by 21 honey-hunters from 2017 to 2022.

Attracting and signalling to honeyguides

Once in an area which honey-hunters considered suitable for locating bees, they started searching visually for bees' nests. While doing so, the honey-hunters attempted to attract honeyguides by making loud 'brrr-hmm' calls (Spottiswoode et al. 2016), as well as sometimes using whistles, loud whoops or chopping sounds to attract honeyguides (Figure 2.3). Honeyguides also readily approached humans even when they were not making specific signals, seemingly recognizing humans as potential cooperative partners and seeking to elicit an interaction (Isack 1987; Short and Horne 2001). On 72 experimental transects to recruit honeyguides in our study area, Spottiswoode et al. (2016) found that honeyguides responded 66.7% of the time to 'brrr-hmm' calls, but honeyguides also responded to human control sounds 33% of the time.

Cooperating with honeyguides

Upon encountering a honeyguide, honey-hunters made the decision of whether to cooperate with the honeyguide (i.e., follow and call to it). Direct observations and conversations with honey-hunters suggested that following a honeyguide without vocalizing may occasionally be successful, but that regular calls to the bird appear to signal that the honey-hunter is following while also communicating the human's relative position to the bird. Although I have not yet analysed data to support this idea, it appeared that regular calls to honeyguides stimulate it into sustaining a loud audible chatter. Shouting, calling, whistling, or chopping sounds directed at a guiding honeyguide are seen across most (likely all) honey-hunting cultures (Friedmann 1955; Isack 1987; Wood et al. 2014; Spottiswoode et al. 2016; van der Wal et al. 2022a; Spottiswoode and Wood 2023).

In Niassa, Yao honey-hunters produced vocal signals at a rate of 6.16 ± 0.87 calls/min (mean ± SE) when 'recruiting' honeyguides, and 7.10 ± 0.44 calls/min (mean ± SE) when following a honeyguide. Vocalizations directed towards honeyguides when recruiting or following them can be broadly classified into one of three types: (1) stereotypical "brrrr", "brrr-hmm" or "brrr-whoo" trill-grunt sounds, (2) talking or singing to the birds using complete Yao phrases, and (3) whistles (Figure 2.3). Stereotypical "brrr-hmm" calls comprised 94.2 % (N = 7,242) of overall sounds directed at honeyguides by honey-hunters when recruiting or following honeyguides, talking or singing sounds comprised 1.8 % of sounds, and whistles comprised 4 % of sounds (Figure 2.3). The honey-hunter leading the party (who was the primary communicator to the honeyguide) produced an average of 177 ± 17.3 calls (mean ± SE) over the course of a cooperative trip with a honeyguide. Such cooperative bouts were on average 26 ± 2.46 minutes long (mean ± SE, n = 41 recordings).

When recruiting honeyguides, Yao honey-hunters projected loud 'brrr-hmm' calls (previously measured at between 74.2–96.5 dB at a range of 3 meters; Spottiswoode et al. 2016) which are expected to be audible above background noise to honeyguides at least 249 m away (Cram et al. 2022). Once a honeyguide arrives, Yao honey-hunters almost always lowered the volume of their vocalizations, producing a more frequent, shortened version of the call (usually the 'brrrr' component). In conversation, Yao honey-hunters reported that their reason for reducing the volume of calls is that "the honeyguide stays closer and doesn't fly too far ahead while following it", "it is easier to hear the bird by calling more quietly to it", or "it is easier to call more often when calling more quietly". This may also make it easier for honey-hunters to detect changes in the honeyguide call to the squeaky 'indication' call, which can signal proximity to a bees' nests (Chapter 4).

On occasion, a honey-hunter (pers. obs.) assessed the behaviour of a honeyguide by following the bird for a short distance, and judged whether it was worth following for a longer distance from the vigorousness and continuity of its chatter, its visibility in dipping flight as it guided, and how quickly the honeyguide to respond to bursts of vocalization by humans. This fascinating aspect of the two-way 'conversational' nature of human-honeyguide cooperation occurred when a honey-hunter, perhaps on losing sight of the guiding bird, suddenly increased the volume of their calls to the bird (effectively shouting at it) using either stereotypical calls or everyday words (or insults) in Yao. In most cases, this shouting resulted in the honeyguide flying back towards the honey-hunter and chattering vigorously, before once again guiding the humans in the direction of bees.

In places where honeyguides are abundant, honey-hunters do not necessarily follow every honeyguide they encounter. In conversation, Yao honey-hunters reported that numerous factors influence their decision of whether to follow a honeyguide: Is the habitat one where finding a bee's nest is likely? Are the trees generally of a harvestable size, or are they all too tall or hard-wooded (e.g., a stand of *Acacia nigrescens*)? Is the honey-hunter prepared to harvest the honey, considering the time of day, availability of water, means to light a fire, and suitable tools for felling or opening a tree trunk (axe or machete)? They reported also sometimes considering recent harvest successes and failures in the area, and the time investment required to follow a honeyguide and harvest a bees' nest, especially if they are walking through a habitat patch to reach another area of the landscape. If a honey-hunter is in an area specifically for the purpose of honey-hunting, they reported that they are far more likely to follow the honeyguide.

Sighting the bees' nest

Honeyguides generally indicated the location of a bees' nest by falling silent in the vicinity of the nest (Friedmann 1957; Isack 1989; Short and Horne 2001). This was sometimes preceded by 'indication' calls (Isack 1987; Chapter 3). In Niassa, Yao honey-hunters placed great confidence in a location they were guided to by a honeyguide, and searched a tree (or trees) in this vicinity for a bees' nest for 15 minutes or more. When a honeyguide guided honey-hunters to bees' nests in rock cavities, much disappointment was expressed by the honey-hunters because many harvests in rock cavities are extremely difficult or impossible to undertake. Isack (1987) reported that bees in rock cavities are also guided to in Kenya. Bees' nests in baobab trees (*Adansonia digitata*) can be similarly inaccessible when inside the trunk, but in Niassa are more commonly located underneath big branches. The location of baobab bee colonies (n = 108 recorded) is usually already familiar to honey-hunters and the bees tend to be present from year to year, but can be too dangerous to harvest during the day and are instead climbed and harvested at night by honey-hunters with the necessary specialised skills.

Honey-hunters reported that on windy days it can be harder to spot the bees' nest due to reduced movement of bees' flying in and out of the tree cavity. We have recorded honeyguides guiding from early in the morning (from 0502 h; Chapter 3) until sunset, but their propensity to guide, and presumably overall activity, dips between 10:00 and 15:00 h (Spottiswoode et al. 2016; Chapter 3). After falling silent at a bees' nest, honeyguides often remained within hearing range, if not in sight. Whether honey-hunters located the bees or not, they often stimulated the honeyguide to resume guiding behaviour by calling loudly or whistling. Honey-hunters often started moving away from the area if the honeyguide did not respond, which sometimes prompted the honeyguide to start chattering and guide them away from the previous bees' nest.

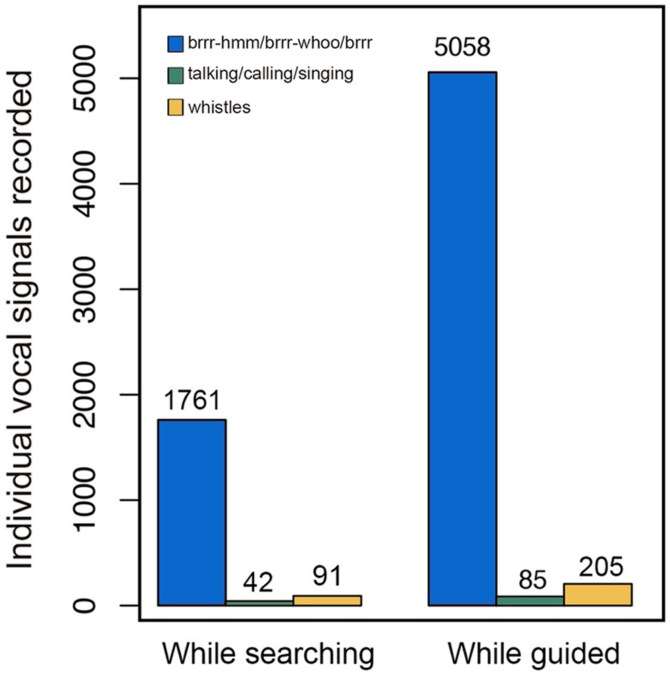


Figure 2.3. In a set of recordings of 10 Yao honey-hunters made over 17.9 hours over 41 honey-hunting trips, honey-hunters predominantly used locally specialised 'brrr-hmm' vocalisations while searching for honeyguides ('recruitment' phase) and whilst being guided by a honeyguide ('following' phase).

Guiding persistence by honeyguides, and disruptions

Cooperative interactions between honeyguides and humans are regularly interrupted by other honeyguides (Isack 1987). Both adult and immature honeyguides guide people, including in Niassa, but we particularly observed interruptions between a guiding adult male honeyguide and another adult male. Sometimes a guiding adult female was interrupted by an adult male, although this appeared to be less common. Such interruptions could take the form of 'competing' guiding behaviour where the second bird also attempted to guide the honey-hunters, or alternatively took the form of chasing (possibly territorial) behaviour where the guiding bird was aggressively chased by the second honeyguide. These interactions could result in the honeyguide disappearing from sight, or temporarily disappearing and returning to guide after an interval of 1–5 minutes. Unless the bird was colour-ringed or individually distinctive in plumage, it could be difficult to detect whether the returning guide is the original bird or the interrupting bird. During cooperative honey-hunts, other honeyguides, especially scaly-throated honeyguides (*I. variegatus*) sometimes followed the cooperative interaction without vocalizing, likely because of the wax reward after a harvest (see also Chapter 3; Cram et al. 2023). Other greater honeyguides (both adult and immature) sometimes also followed honey-hunts without vocalization and interruption, but were generally very inconspicuous.

Division of labour amongst Yao honey-hunters

Over 10 days on two multi-day honey-hunting trips with four honey-hunters in June 2018 and July 2019, and on numerous other single day-honey honey-hunts, I observed that the responsibility of calling to honeyguides was shared amongst the honey-hunters (taking turns to lead). Once a honeyguide started guiding, the person calling at the time would call to and follow that bird until they found a bees' nest, or until cooperation failed. In optimal habitat for bees, the honey-hunters often walked in a line abreast 50–200 m apart from each other, with usually two or more people calling to honeyguides simultaneously. After a honeyguide started guiding, all but the honey-hunter closest to the bird would go quiet, and all would converge on following the guiding bird.

Male and female honey-hunters all participated in calling to honeyguides, and carrying harvested honey, food and other equipment. Female honey-hunters also participated in cutting down trees and opening tree cavities to access honey. Honey-hunters from Mbamba reported that they plan multiple multi-day honey-hunting trips based on prior knowledge of areas of the landscape which they consider to be less intensively harvested, and which contain a water source (e.g., seasonal river, spring or perennial river). Water was important to honey-hunting groups for hydration, but also as a means of washing off and cleaning up the sticky mess which is left behind after pulling honeycomb out of tree cavities. Honey-hunters reported that they sometimes leave areas of the landscape in which they see fresh signs of other honey-hunters, considering such areas to be depleted.

Seasonality and habitat used for honey-hunting

Interactions between honeyguides and humans varied significantly in number through the year (Rao's Spacing Test: $t = 357.2$, $p < 0.001$), with bimodal peaks in May–June and October, though the latter peak was not evident in all years (Figure 2.4). The end of the rains in May or June coincides with increased flowering and nectar flow for bees, and it was during this period when most bees' nests were found. Circular statistics revealed a mean (across 2017–2022) peak of bees' nests harvested on the 30th of June. Fewer bees' nests were found and less human investment in honey-hunting occurred in the wet-season months of February and March, and the dry season months of August and December (Figure 2.4). Honey-hunters used the landscape in all directions from Mbamba village (Figure 2.2) but used a much smaller overall area for honey-hunting in the wet season (274 ± 63.0 km^2; mean ± SE) compared to the dry season (613 ± 55.2 km^2; mean ± SE) (Figure 2.5). The total area visited for honey-hunting fluctuated from year to year, but overall declined slightly between 2017 and 2022.

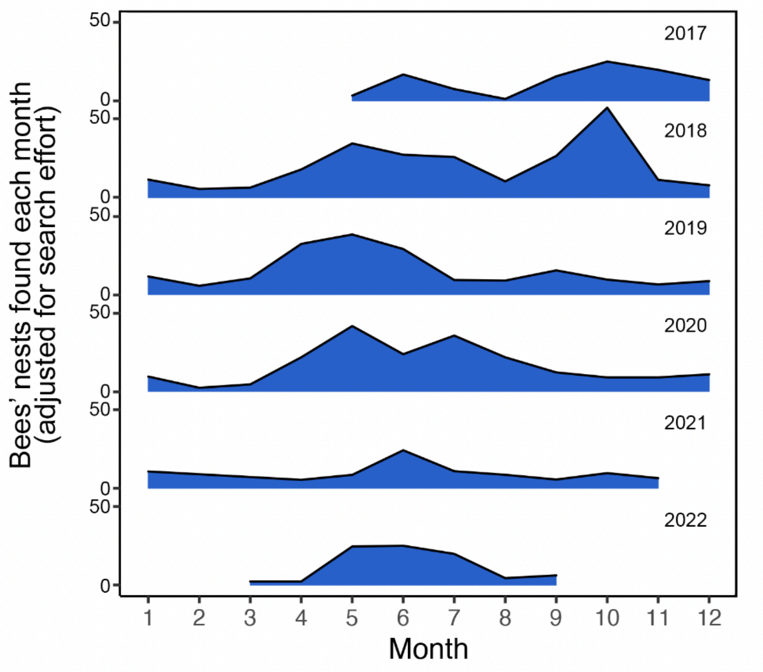


Figure 2.4. The number of bees' nests found per month by honey-hunters varied through the year. The number of bees' nests found is adjusted to the maximum number of honey-hunters (n = 21) collecting data each month, since the number of honey-hunters ranged between 14 and 21 during different parts of the study.

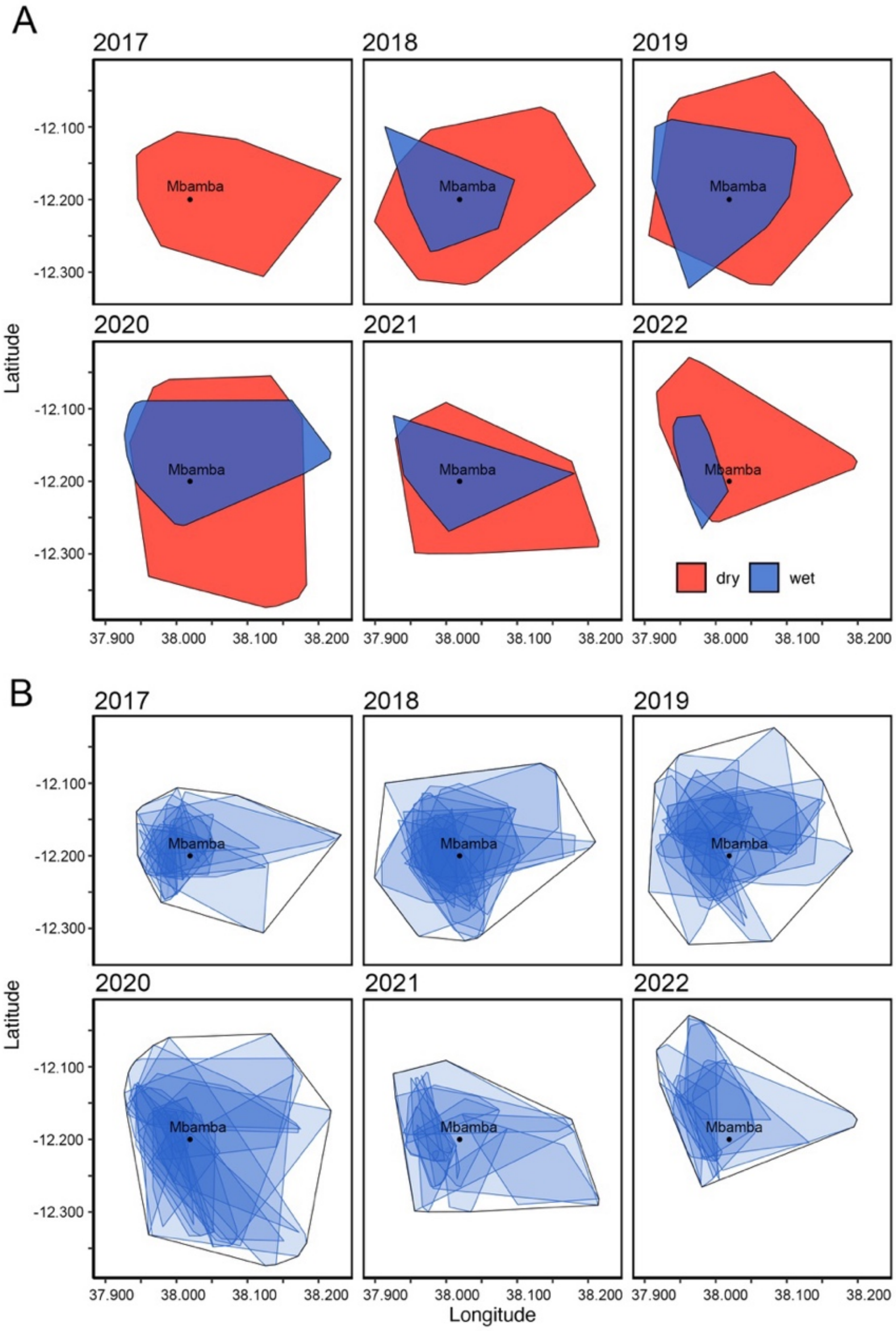


Figure 2.5. (A) Seasonal differences in landscape use by 21 Yao honey-hunters between 2017 and 2022. Maximal convex polygons (MCPs) of areas visited are shown in blue for the wet season (January to May) and red for the dry season (June to December). (B) Annual variation in landscape use by each of 21 Yao honey-hunters between 2017 and 2022. Each blue shaded MCP corresponds to the area visited each year by a single honey-hunter, surrounded by the total area visited by all honey-hunters (black line).

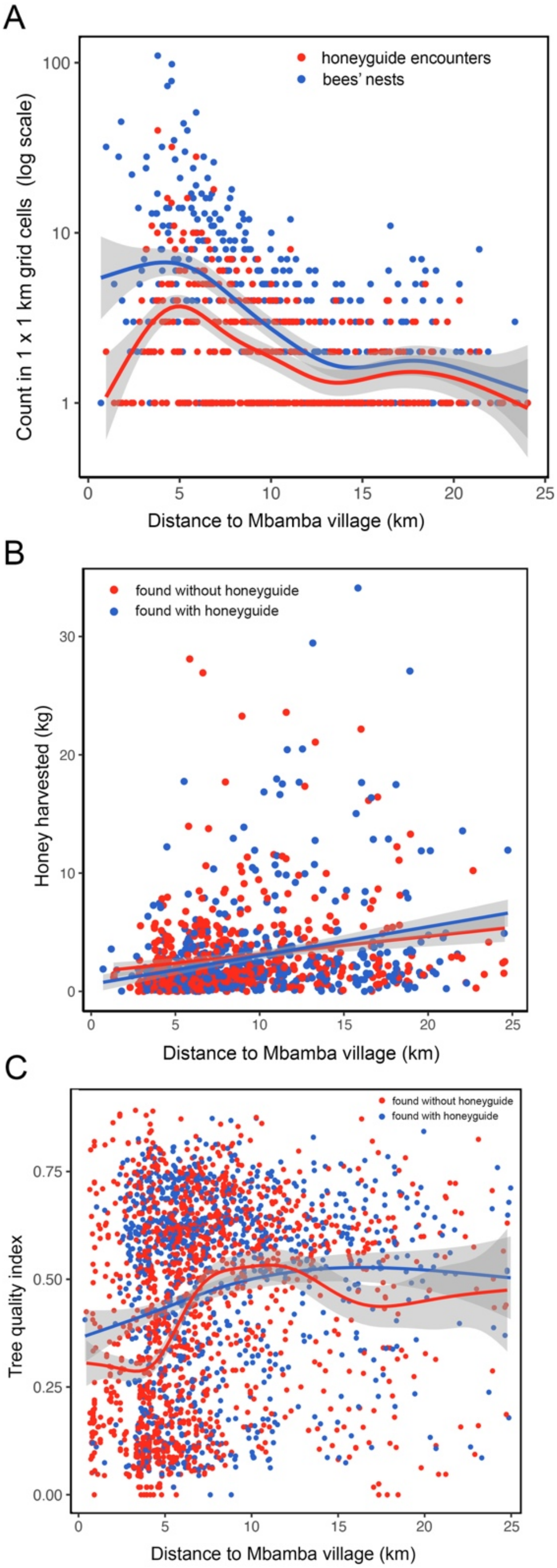

A
Count in 1 x 1 km grid cells (log scale)
100
10
1
honeyguide encounters
bees' nests
0
5
10
15
20
25
Distance to Mbamba village (km)
B
Honey harvested (kg)
30
20
10
0
found without honeyguide
found with honeyguide
0
5
10
15
20
25
Distance to Mbamba village (km)
C
Tree quality index
0.75
0.50
0.25
0.00
found without honeyguide
found with honeyguide
0
5
10
15
20
25
Distance to Mbamba village (km)

Figure 2.6. (A) Number of guiding interactions and number of bees' nests found with and without honeyguides in 1 km^2 grid cells around Mbamba village in relation to distance to village. Fitted curves are derived from generalized additive models (GAMs) (both are significant with an overall negative slope). (B) Quantity of honey harvested (kg) relative to distance to village, with and without the cooperation of honeyguides (represented by blue and red dots, respectively). (C) Predicted values and fitted curves from a GAM model of the quality of bee trees, found with and without the cooperation of honeyguides (represented by blue and red dots, respectively) in relation to the distance from Mbamba village.

How to be a honeyguide

Here I evaluate against available field data six attributes and behaviours of honeyguides expected to contribute to successful mutualism with humans: that honeyguides should (1) be found in any part of a landscape with wild bees' nests; (2) directly guide humans to bees' nests and know where bees' nests are located; (3) successfully guide humans to bees' nests more often than they fail; (4) significantly increase the rate at which bees' nests are found; (5) guide to multiple bees' nests if the first one is not harvested; and (6) guide humans to bees' nests in trees amenable to harvest. I found that:

(1) Honeyguides were found in almost any area of the landscape containing wild bees' nests and were not recorded guiding humans close to the village, where the most trees have been cleared for agriculture (Figure 2.2). Peak human-honeyguide interactions occurred around 5 km from Mbamba village (Figure 2.6A). The number of bees' nests found and number of interactions with honeyguides proportionally reduced in a very similar way with distance from beyond 7 km (Figure 2.6A). Had we not observed this proportional reduction, it would have indicated that some parts of the landscapes have bees but not honeyguides.

(2) Overall, honeyguides guided people to bees' nests with remarkable directness (Figure 2.1), over a wide range of distances ranging from less than 50 m to 2,000 m (Figure 2.1). After starting to follow a honeyguide, honey-hunters walked a mean of 553 ± 19 m (mean ± SE) until they found bees. Such bees' nests took on average 17.1 ± 0.61 (mean ± SE) minutes to walk to and find. The directness of most guiding interactions demonstrates that honeyguides had prior knowledge of where bees' nests were located, and often guided there without needing to 'refresh' their position by flying ahead to the bees in order to determine which direction to guide in.

(3) Over the course of five years of data collection, honeyguides successfully showed humans bees' nests more often than they failed: of 2,399 separate guiding interactions recorded, 1,463 resulted in finding at least one bees' nest (61 %), and 936 interactions resulted in failure to locate a bees' nest (39 %). The exact reasons for failure were not recorded in the application data-collection system but based on our direct observations during fieldwork, failure to find bees can be caused by a wide range of factors. For example, humans sometimes failed to spot the bees' nest once they arrive near it, or the honeyguide was sometimes disrupted by other honeyguides whilst guiding (see above) or simply went silent while guiding.

(4) When humans did cooperate with honeyguides, they found bees' nests at a much higher rate (per unit time of searching) than when searching for bees' nests without the cooperation of honeyguides (Linear mixed-effects model: estimate = 12.82, SE = 1.61, $F_{1,41}$ = 63.75, $p < 0.001$; Figure 2.7A). Honey-hunters located a bees' nests at a rate of between 5.7 and 38.5 per hour of following a honeyguide, versus between 0.08 and 0.7 per hour when not cooperating with a honeyguide (n = 1,463 bees' nests; Figure 2.7B). Honey-hunters also walked less far per bees' nest found with the cooperation of a honeyguide (0.2 ± 0.02 km; mean ± SE). compared to the distance walked per bees' nest found without the cooperation of a honeyguide (10.4 ± 1.62 km; mean ± SE) (Linear mixed-effects model: estimate = 10.16, SE = 1.62, $F_{1,41}$ = 39.24, $p < 0.001$; Figure 2.7). Overall, the total number of successful interactions with honeyguides per day significantly predicted the total honey yield obtained per day of honey-hunting (quasi-Poisson regression: estimate = 0.032, SE = 0.003, t = 10.31, $p < 0.001$), indicating that honey-hunters gained an increase in honey yield from cooperating with honeyguides (Figure 2.8). Overall, honey-hunters found 39.3 % of bees' nests with the cooperation of honeyguides and 60.7 % of bees' nests without being guided, over 5 years (n = 2,703 bees' nests).

(5) The ability of a honeyguide to guide to multiple bees' nests if the first one is not harvested is a characteristic of honeyguide behaviour I directedly observed on n = 15 occasions. We were unable to collect reliable data on this using the data-collection application because it requires individual recognition of honeyguides, and this can be difficult without binoculars (which honey-hunters did not carry), and in some cases it requires colour-rings to be certain a second bees' nest involves the same honeyguide individual if two birds are of the same age, sex, and in the same area at the same time.

(6) Honeyguides guided honey-hunters to many trees with bees' nests suitable for harvest. Honey-hunters were significantly more likely to harvest honey from trees with a bees' nest found

with the cooperation of a honeyguide (51.2 % of bee trees harvested when found with a honeyguide) compared to bees' nests found without the cooperation of a honeyguide (31 % of trees harvested) (n = 1,068, 1635, $\chi^2 = 115.32$, df = 1, p-value < 0.001, Figure 2.9). The 'quality' (from a human perspective) of bee trees was found to increase with distance from Mbamba village (GAM, with a binomial family and a logit link function; n = 1,061, edf = 1.027, df = 1.053, $\chi^2 = 29.27$, $p < 0.001$; Figure 2.6). Within 7 km from the village, honeyguides guided honey-hunters to trees which ranked higher in quality than those found without honeyguides (Figure 2.6). Beyond 15 km from the village, bee trees which were found without honeyguides were as variable in quality as those found with the cooperation of a honeyguide (Figure 2.6). Tree size (measured as diameter at breast height) and the weight of honey harvested were significantly positively correlated (GLMM, estimate = 0.011, SE = 0.002, Z = 5.691, $p < 0.001$). Trees found with the cooperation of honeyguides did not, on average, yield more honey than those found without honeyguides (GLMM, estimate = -0.105, SE = 0.069, Z = -1.501, p = 0.133).

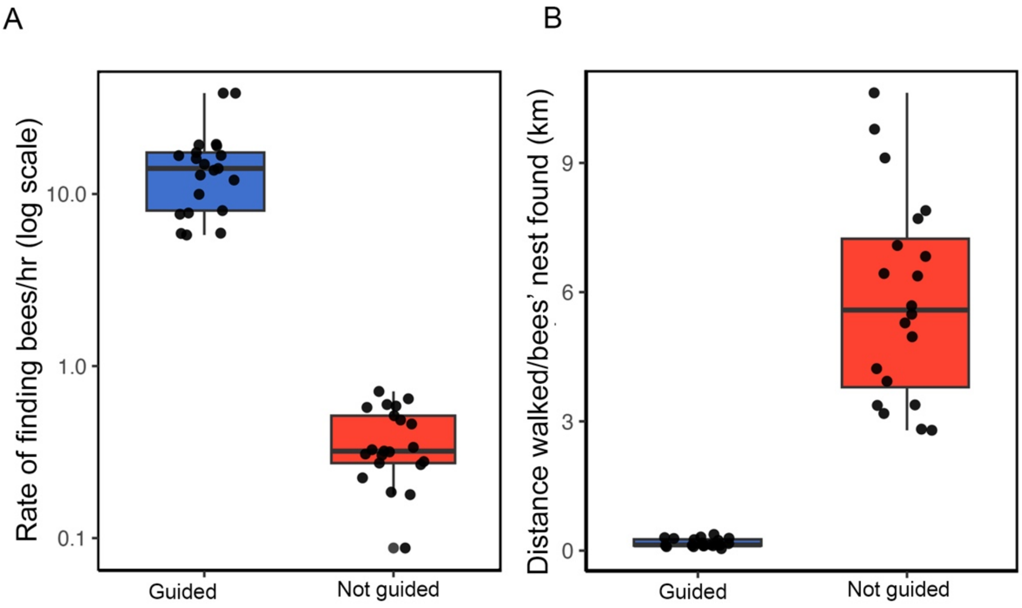


Figure 2.7. (A) Yao honey-hunters found bees' nests at a higher rate per hour when cooperating with a honeyguide and (B) covered less distance per bees' nest found whilst doing so, than when finding bees' nests without the assistance of a honeyguide. Each datapoint is a honey-hunter level cumulative value (i.e, the mean value for all trips by an individual honey-hunter, for 21 honey-hunters, derived from the honey-hunting trips which yielded 1,463 bees' nests).

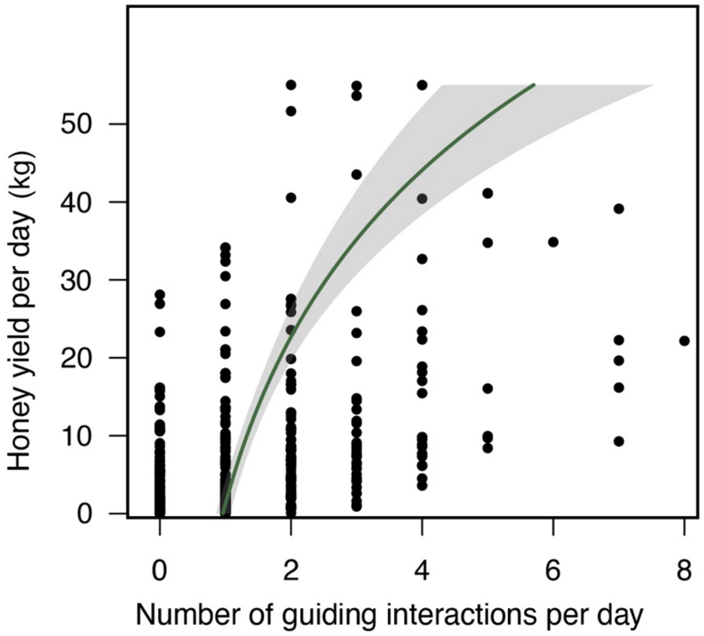


Figure 2.8. The total number of successful interactions with a honeyguide, per day, was significantly related to the total honey yield obtained per day of honey-hunting (quasi-Poisson regression: estimate = 0.032, SE = 0.003, t = 10.31, $p < 0.001$). Predicted values from the regression are plotted as a green line with SE shaded grey. Each data point is the yield from a single honey-hunting excursion on a unique day between 2017 and 2022.

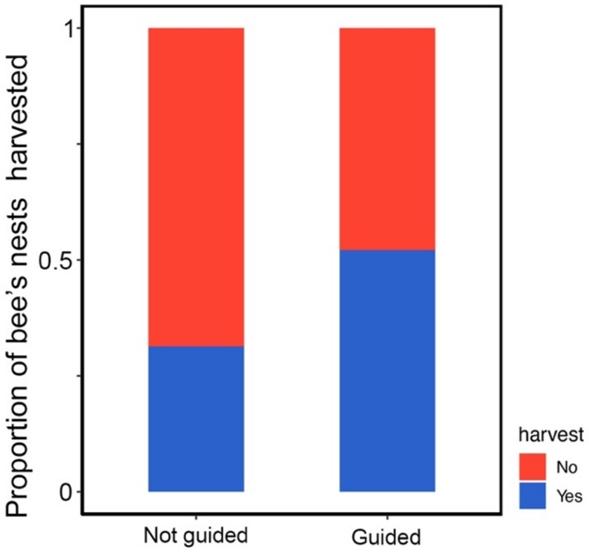


Figure 2.9. Yao honey-hunters were more likely to choose to harvest bees' nests which they found with the cooperation of honeyguides, than those which they found on their own (n = 1,068, 1635, χ^2 = 115.32, df = 1, p-value < 0.001).

Part 2: Does asymmetry in rewards from cooperation lead to a conflict of interests?

I found that after harvests, honey-hunters on average left behind 0.47 kg of wax (n = 997, 95 % CI = 0.43, 0.52) (which photos collected in the data-collection app showed to be a mixture of new and old honeycomb, containing a variable quantity of bee larvae and pollen). Honey-hunters left behind similar quantities of wax after harvesting a bees' nest they were guided to by a honeyguide, compared to a bees' nest they found by themselves (Figure 2.10; GLMM, estimate = -0.090, SE = 0.069, Z = -1.296, p = 0.195). More wax was left behind after harvesting bees' nests located in larger trees (measured as diameter at breast height) (GLMM, estimate = 0.004, SE = 0.001, Z = 2.264, p = 0.023). A Spearman's rank correlation revealed a significant positive relationship between honey and wax yields from harvests (Spearman's ρ = 0.28, 95% CI: 0.23, 0.34, $p < 0.001$).

I found that the overall mean honey yield per harvest for Yao honey-hunters (with a variable amount of wax and brood mixed in) was 3.01 ± 0.12 kg (mean ± SE), regardless of whether or not the bees' nest was found with the assistance of a honeyguide: the mean honey yield for bees' nests found with the assistance of a honeyguide (2.94 ± 0.17 kg; mean ± SE), was very similar to that for bees' nests found without a honeyguide (3.09 ± 0.16 kg; mean ± SE) (Figure 2.10). Only 0.3 % (n = 3 of 1,068) of harvests resulted in zero measurable honey for the honey-hunting party. Note that the per capita reward is usually smaller than the means above, since harvested honey is often divided amongst the members of the honey-hunting party.

I found that the honey yield for honey-hunters was significantly more variable (standard deviation = 4.05) than the (measured) wax yield for honeyguides (standard deviation = 0.77) as determined from bootstrap resampling, where the 95 % confidence interval for the difference in standard deviations between honey and wax ranged from 2.632 to 3.658. Because this interval does not encompass zero, the honey and wax gains are significantly different in their variability.

Based on the scenarios laid on in Table 2.1, I tested whether honeyguides or humans more often lost out from an interaction (– result for honeyguides, + result for humans or vice versa). I found that the percentage of harvests for which honeyguides benefited from a reward and humans did not was 9.8 % (105 of 1,068). In contrast, humans benefited, and honeyguides did not, at 6.8 % of harvests (73 of 1,068), although the true value is likely lower since honeyguides may benefit simply from a harvest occurring, even if no measurable wax reward is actively left by the honey-hunters (Figure 2.11). When compared statistically, I found a significant difference between the number of bees' nest harvests from which one partner gained and the other did not (mixed-effects logistic regression model: estimate = 0.697, Z = 2.111, p = 0.034) (Figure 2.11). In this model, honey-hunter identity was also influential (variance = 1.268, standard deviation = 1.126), indicating that honey-hunters varied considerably in how likely they were to leave a wax reward. Overall, ‘conflicting’ outcomes from honey-harvests only represented 16.6 % of all harvests (Figure 2.11). In 95.3 % of harvests, at least one partner measurably benefitted, and in only 4.7 % of harvests did neither partner measurably benefit.

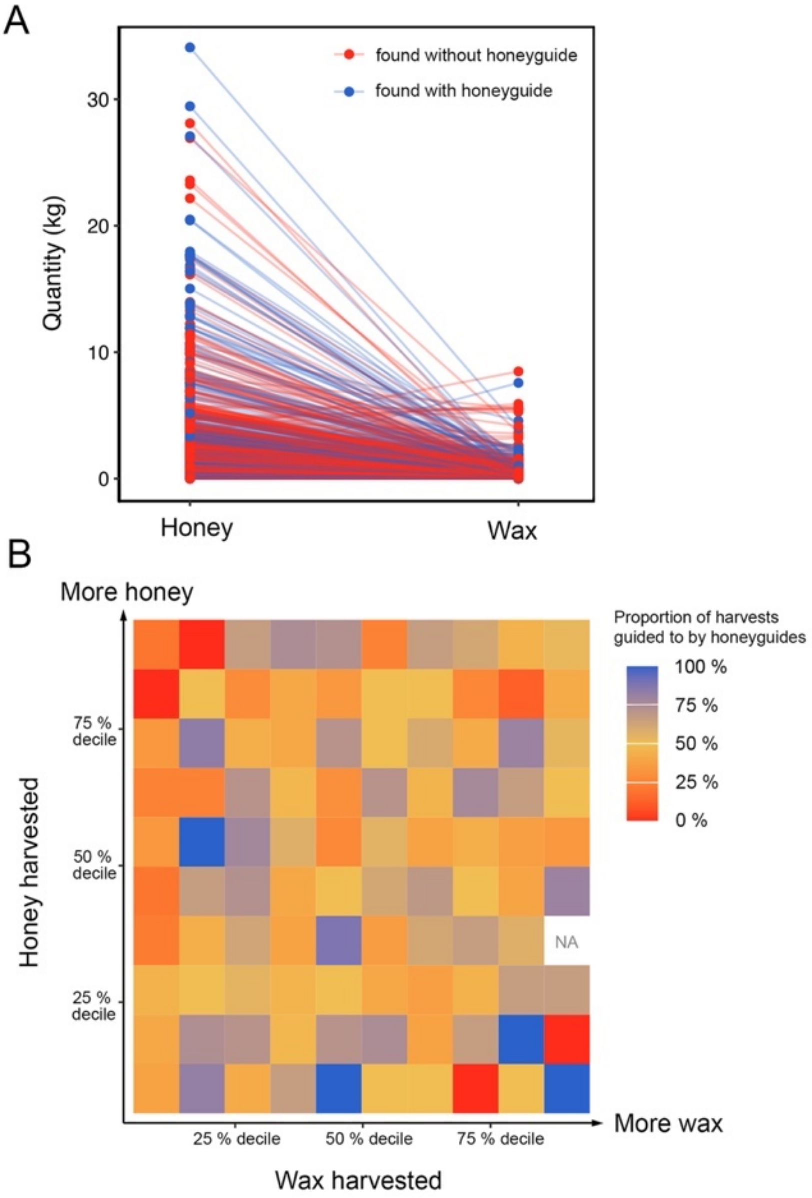


Figure 2.10 (A) The honey benefits to humans and wax benefits left behind for honeyguides following bees’ nest harvests (both expressed in kilograms), at n = 997 bees’ nests harvests. Yields measured from the same harvest are linked with straight lines (red represents bees’ nests found

without honeyguides, and blue lines represent bees' nests found with a honeyguide). (B) Harvests at bees' nests found with honeyguides were not overall more likely to yield a larger quantity of honey or of wax than those found without honeyguides. If this were the case, then we would expect the heatmap to be distinctly more blue on the top or right-hand side respectively.

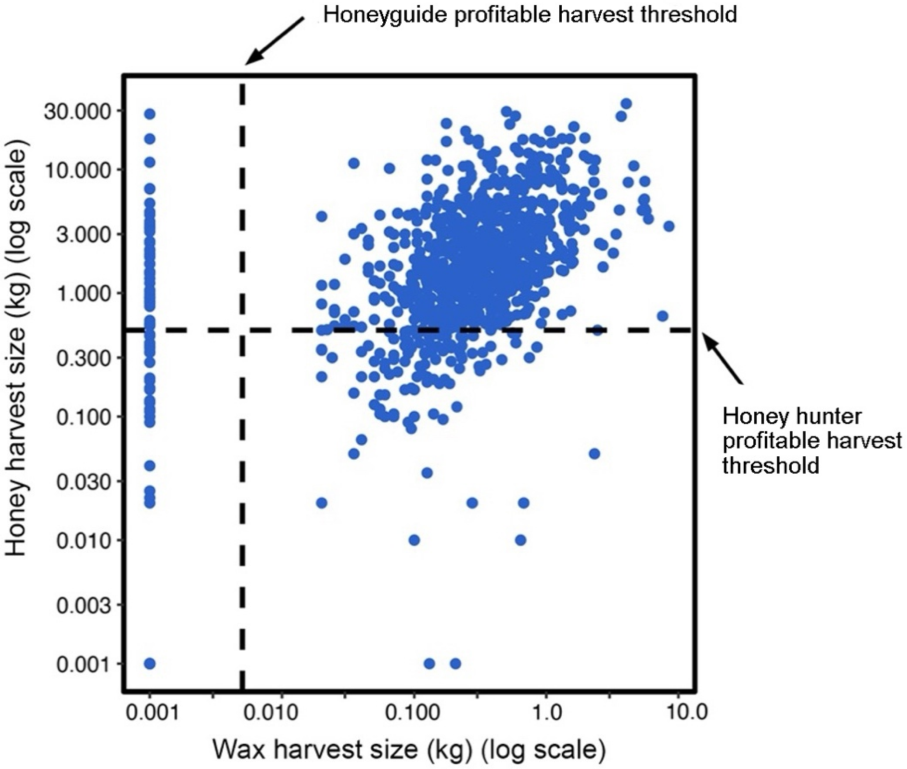


Figure 2.11. Honey and wax yields measured from 986 bees' nest harvests (log scale used for clarity). The thresholds of profitable harvests, beyond which either humans (dashed horizontal line; set at 0.5 kg) or honeyguides (dashed vertical line; set at 5 g) are assumed to gain a measurable benefit from the harvest are marked.

Discussion

In this chapter, I provide a detailed account of the 'where' and 'how' of human-honeyguide cooperative interactions in Niassa, enabled by collaborative data collection with Yao honey-hunters. This research drew on a five-year dataset, encompassing over a thousand natural interactions between humans and honeyguides across >800 km^2 of miombo woodland in northern Mozambique, and so represents a substantial contribution to understanding honeyguide behaviour and ecology over longer time scales and across a broader geographical area than previously studied. While this chapter does not redefine the fundamental principles of guiding interactions as documented by previous studies (particularly Isack 1987), it presents some novel insights.

The first key finding is that honeyguides and their interactions with humans are widespread across the landscape, rather than being confined to areas with higher bee densities (Figure 2.2). This broad distribution makes it beneficial for humans to signal and attempt to recruit honeyguides almost anywhere within their 30 km foraging radius of Mbamba village (Figure 2.2) and to persist in doing so year after year. Such availability of mutualistic partners is not a guaranteed feature elsewhere in Africa, especially as the mutualism declines or has already vanished from much of Africa due to the reduced availability of, or access to wild bees' nests, and reduced desire for cooperation by humans (Isack 1999; van der Wal et al. 2022).

The second key finding was a broad estimation of the overall success and failure rates of human and honeyguide interactions. I found that of over 2,399 separate guiding interactions, 1463 resulted in finding bees (61 %), whereas 936 interactions resulted in failure to locate bees (39 %). The reasons for failure are numerous, and require further investigation, but based on first-hand experience, failure to find bees can be caused by a wide range of factors. For example, the honey-hunters may fail to spot the bees' nest once they arrive near it, the honeyguide may get disrupted by other honeyguides whilst guiding and disappear, or simply goes silent while guiding for no detectible reason. Crucially, however, cooperation with humans was successful more often that it failed: after finding a bees' nest, honey-hunters were 65.8% more likely to harvest the bees if they found a bees' nest with a honeyguide (increasing from a likelihood of 31.5% when finding bees without a honeyguide, compared to 52.2% with a honeyguide) (Figure 2.9).

The exact reasons for this are discussed in greater depth in Chapter 5, but briefly, are likely due to the ability of honeyguides to help humans find bees' nests that are consistently overlooked by humans searching alone (likely aided by the fact that honeyguides can fly), and because honeyguides tend to guide humans to smaller-stemmed (and so more readily harvested) trees with bees' nests than those found without honeyguides (see Chapter 5). Although people were more likely to harvest bees' nests they had been shown by honeyguides, these nests were not individually higher-yielding than bees' nests that people found by themselves. This contrasts with the findings of Wood et al. (2014) who showed that Hadzabe hunter-gatherers obtain significantly more calories from honeyguide-shown bees' nests than from bees' nests they find on their own. One possible reason for this is that Hadzabe honey-hunters appear to more frequently revisit bees' nests that they already know the location of (Wood et al. 2014), compared to Yao honey-hunters, and may receive lower yields from such self-found nests versus previously unknown nests shown to them by honeyguides.

In the study most comparable to this chapter, Wood et al. (2014) investigated the influence of honeyguides on the rates of finding bees' nests among the Hadzabe people. They found that Hadzabe honey-hunters' rates of finding bees' nests increased from 0.5 bees' nests per hour of searching without honeyguides, to 3.3 per hour of searching when following a honeyguide. For comparison, in this study I found that Yao honey-hunters' rates of finding bees' nests increased from between 0.08 and 0.7 per hour of searching without honeyguides, to between 5.7 and 38.5 per hour when following a honeyguide. This suggests that some Yao honey-hunters in Niassa appear to benefit even more from cooperation with honeyguides than Hadzabe honey-hunters do. This may be because Yao honey-hunters tend to revisit fewer bees' nests which they have prior knowledge of, and also encounter honeyguides at a higher rate in the landscape compared to Niassa (Spottiswoode and Wood 2023).

In both this chapter and in Wood et al. (2014), there are complications in how time is partitioned for these calculations of rates of finding bees' nests. Fine-grained divisions of time spent by honey-hunters doing activities such as preparing a fire before harvest, chopping the tree, cleaning or processing honey in some way (e.g., squeezing honey into buckets if there is not sufficient space), time spent resting and recovering from bee stings or long walks were not well captured in the app dataset. This impacts the calculation of rates (particularly without honeyguides) because these time denominator measures are not equally distributed. For example, while time spent doing the above activities may have been included in the time denominator for time spent searching without a honeyguide, it was certainly not included in the time when a honey-hunter was following a honeyguide, because when following a honeyguide that is usually the only activity undertaken. A further issue is that time spent moving into an area which allows for more honeyguide encounters is not factored into the time (i.e., costs) invested into honeyguide cooperation. Together, these issues allow considerable scope for fine-tuning how we estimate how much honeyguides help.

A related issue arising from estimation of rates can be found in Spottiswoode and Wood (2023), who estimate that a honey-hunter who changed their whistled signal to a trill-grunt in the Hadza region would find less than half as much honey. Their expected intake rates were calculated by multiplying rates of response by honeyguides over 30 minutes to local versus foreign signals by the rates of foraging success with and without honeyguides (0.5 bees' nests per hour without versus 3.3 per hour; Wood et al. 2014). What these expected intake rates did not account for were the overall true number of encounters between honeyguides and humans during a foraging day (in which a rate of 3.3 bees' found nests per hour is only realized for 3 percent of total foraging time; Wood et al. 2014). The cost to Hadzabe honey-hunters of switching from local to foreign signals is therefore less likely than the > 50 % decrease estimated, once biologically relevant human-honeyguide encounter rates are accounted for. Future calculations of expected intake rates in the human-honeyguide mutualism should ideally include daily rates of honeyguide-human cooperation as well as harvest bout duration (time which is not spent foraging), measured under the same ecological and behavioural conditions.

Such varying estimates exemplify the issues faced in calculating rates of success with and without honeyguides, and the knock-on implications when these rates are used to estimate payoffs to humans under varying hypothetical scenarios. Accurately estimating payoffs from these mutualistic interactions is critical to our understanding of how a geographic mosaic of human-honeyguide signals (Spottiswoode and Wood, 2023) may be maintained despite the widespread movement of people and potentially rapid transfer of human cultural knowledge.

Guiding behaviour and avian spatial cognition

Using GPS data, I found that honeyguides in Niassa guided humans to bees' nests over a mean human walking distance of 553 ± 19 m, in a generally straight heading (Figure 2.1). Like animal migration and food-caching behaviours, guiding behaviour appears to require advanced spatial cognition from honeyguides. To be a functional guide, a honeyguide must remember and recall the locations of unharvested bees' nests and be able, upon encountering a human at a non-predetermined location in the landscape, to know their position relative to their destination and guide in the correct direction. The overall rate of successful interactions indicates that honeyguides are highly capable of this, although how this information is stored within 'cognitive maps', and for how long, is unknown. We also do not know how many bees' nests are stored in the spatial memories of honeyguides, nor how they select which bees' nest to guide a human to, but future work using light geo-tracking tags should readily reveal this.

In addition to guiding, we know that honeyguides are heavily reliant on their spatial memory in two other ways. Both sexes cache high-quality pieces of beeswax (Isack 1987; Chapter 3), and because they are brood parasites, females must locate and relocate numerous nests of their host species (Spottiswoode and Koorevaar 2012). The honeyguide foraging system has intriguing parallels to systems of caching and food retrieval found in other groups of birds which annually find, hide, and retrieve thousands of food items, termed 'scatter hoarding' (Clayton et al. 2007; Vander Wall 1990).

Scatter-hoarding birds sometimes make spatial errors, and it is likely that honeyguides do so too. Of the 936 interactions recorded here which resulted in failure to locate bees (39 % of all interactions), we do not know how many are the result of spatial recall errors (i.e., forgetting where the bees' nest is) versus other causes of failure such as interruptions caused by other honeyguides. I propose in Chapter 4 that honeyguides do make spatial recall errors particularly when they guide humans to destinations other than bees' nests. Errors in retrieving spatial information about food have been measured in detail in scatter-hoarding bird species (Pravosudov & Roth 2013; Sonnenberg et al. 2019) and variation in spatial cognition has been shown to influenced by environmental complexity (Branch et al. 2022; Roth et al. 2012), sleep (Rattenborg et al. 2011), and hippocampal neurogenesis (Leuner et al. 2006). Furthermore, genetically-linked variance in spatial recall errors has been shown in scatter-hoarding, free-living mountain chickadees (*Poecile gambeli*), demonstrating that spatial cognitive ability is available for natural selection in these species (Branch et al. 2022; Welkin et al. 2024). It is therefore plausible, given the key role of spatial information in honeyguide ecology, that honeyguides: 1) have genetic variation in their spatial cognitive ability, and 2) that selection acts to reduce spatial error rates (discussed more in Chapter 4).

Do asymmetric benefits from human-honeyguide cooperation lead to mutualistic breakdown?

At the start of this chapter, I proposed that a readily identifiable conflict of interest may exist in the human-honeyguide mutualism because of the differing benefits each partner gains from interacting (Table 2.2). To effectively benefit from an interaction, honeyguides only need a bees' nest to be harvested and tiny quantity of wax to be left behind (Chapter 3; Diamond and Place 1988; Isack 1987; Dean et al. 1990). Like many other organisms, human foragers sometimes seek to maximize the rate at which they acquire food resources whilst minimizing the energy used to locate and harvesting bees' nests (Wood et al. 2014; Marlowe et al. 2014; Koster and Bird 2024). Therefore, for a human, only a harvestable bees' nest containing substantial quantities of honey is enough for the benefit to exceed the energetic cost of harvesting (Table 2.1). In Niassa I found asymmetry in the rewards gained by each partner (Figure 2.11), but conflicting outcomes only occurred for a small proportion of total interactions.

I found that for the majority of honey harvests (78.8%), both humans and honeyguide partners benefited; for 9.8% of harvests, honeyguides benefited while honey-hunters did not; and for 6.8% of harvests, humans benefited while honeyguides did not measurably do so. For only a small proportion of harvests (4.7%) did neither partner gain a measurable reward. The average quantity of wax left behind, 0.47 kg , was vastly more than that required to satiate a guiding bird (itself weighing only ~0.05 kg). This left much excess available for caching for future consumption by the guiding bird (Chapter 3; Isack 1988), for consumption by "scrounger" honeyguide individuals (Chapter 3, Cram et al. 2023), and for consumption by mammalian wax-eaters (Chapter 3). The quantity of wax left for honeyguides varied considerably between individual honey-hunters, most likely because honey-hunters varied in their personal preference for eating honeycomb containing bee brood as well as honey, and perhaps energetic requirement to do so. The amount of wax comb (often containing bee larvae) left behind appeared to be unrelated to whether a honeyguide had assisted in finding the bees' nest, suggesting that honey-hunters did not make a point of leaving abundant rewards for a guiding bird. Instead, the quantity of wax left behind was simply a function of the size of the tree from which honey was harvested, likely due to the greater capacity of a large-stemmed tree to accommodate wax combs (Figure 2.10A). This implies that honey-hunters simply left behind whatever wax was available. Rewards to honeyguides being cost-free to humans supports the pseudo-reciprocal nature of the mutualism.

Overall, the yields from harvests, relative to body size and therefore energetic costs, were much more variable for humans than for honeyguides. The variability in honey yield from bees' nests that honey-hunters have chosen to harvest suggests that they are unable to accurately predict what they will gain from a harvest. This implies that even if the benefits from a harvest are asymmetrical, opting to cooperate rather than not cooperate with honeyguides is more beneficial over time, so long as benefits exceed costs *on average*. The fact that the mutualism continues to thrive on an everyday basis is itself evidence that the human-honeyguide mutualism in Niassa does not appear to be functioning in unstable manner, where pays either partner to choose non-cooperation (when given the opportunity to cooperate).

As in all mutualisms, there is the ever-present risk that one partner overexploits the other, or abandons their partner (Ferriere et al. 2002; Sachs and Simms 2006). Due to the pseudo-reciprocal nature of human-honeyguide mutualism, neither appears to be the case in this system because neither partner can coerce the other into cooperation, and the rewards (honey and wax) are not directly produced by the mutualists themselves, which greatly reduces the costs to either party of non-cooperation, or failed cooperation. This is as predicted in game-theoretic models of mutual helping (Bshary et al. 2016).

How to be a honey-hunter? Future application of ecological foraging models

This chapter and the above dataset on honey-hunter interactions with honeyguides have largely been addressed from the cost-benefit perspective taken within the mutualism literature. There exists another literature, set of perspectives, and analytical approaches which will likely yield further insights into human-honeyguide interactions. It is that of foraging ecology (Stephens and Krebs 1986; Koster and Bird 2024).

Yao honey-hunters are central-place foragers for much of the year, and unlike hunter-gatherer cultures such as the Hadzabe (Wood et al. 2014) are also horticulturalists and fishermen, making them comparable to the Bolivian cultural group, the Tsimane, in their subsistence strategies (Kraft et al. 2021). Numerous foraging models have been developed for humans and non-humans to explain foraging patch selection, the trade-offs involved in where and when to forage, and which resources to pursue and which to ignore (Koster and Bird 2024). Simple foraging models are usually based on the premise that humans are attempting to maximize the rate at which they acquire food resources (Koster and Bird, 2024) and these rates are often formulated as energy (or kilocalories) acquired per unit of time. Therefore, measuring the quantity of resources gained and time invested in gaining them are both important considerations, as I have highlighted above in my critique of how I and others have calculated the relative benefits of cooperating with honeyguides.

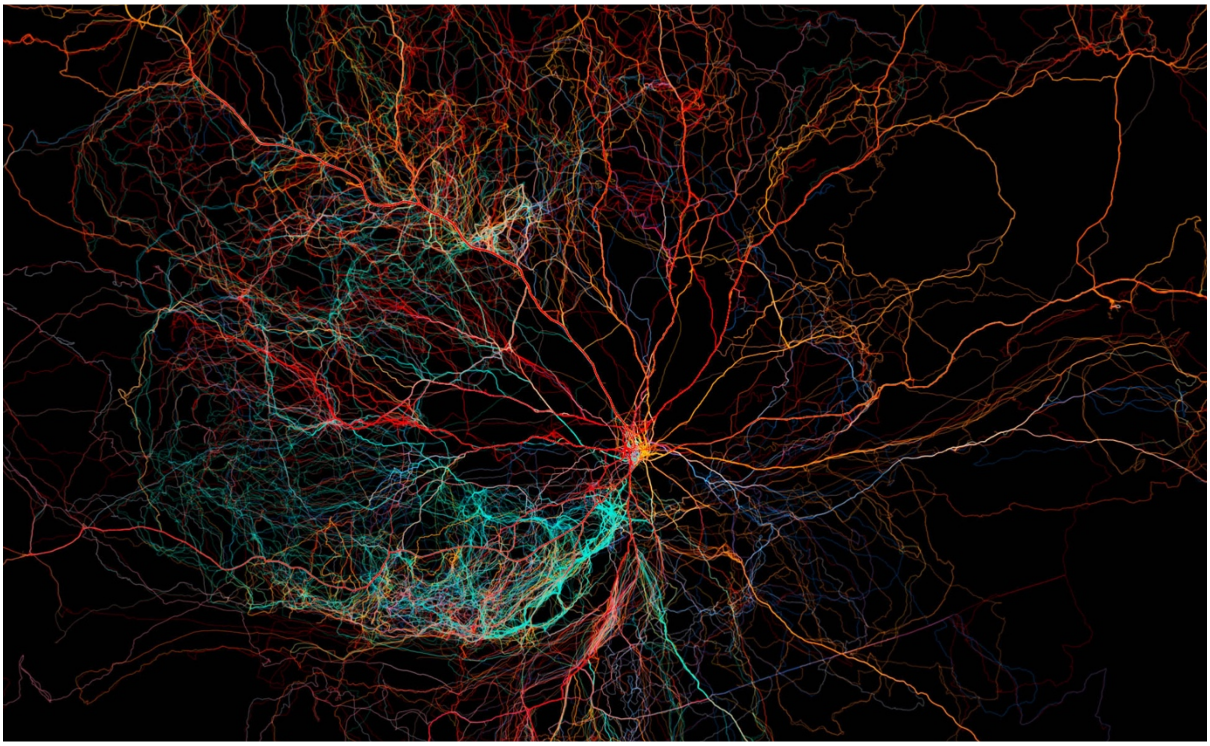
Yao honey-hunters, like other human foragers in the past and present (Kraft et al. 2021), face a number of energetic and time costs: for example, they must walk away from the village to productive foraging patches (Figure 2.2), sometimes needing to expend the energy to cross a river or go around a mountain to do so. The harvest of bees' nests uses axes, which require time and effort to create and maintain, as well as the effort involved in using them in a harvest (Kraft et al. 2021). A key concept in optimal foraging models (and one which is applicable to Yao honey-hunters) is the concept of opportunity costs whereby an individual, by choosing one of multiple options (e.g., following a honeyguide), trades that decisions off with the opportunity to take another option (e.g., search for bees without the cooperation of honeyguides, travel between habitat patches, or engage in fishing or other livelihood activities) (Stephens and Krebs 1986).

Humans are a tractable species in the study of mutualism whereby motivations, preferences, and habits can be easily probed, and behaviour experimentally manipulated with relative ease compared to other mutualistic systems. Humans, however, sometimes choose to forgo short-term benefits in favour of long-term ones, thus bringing greater complexity to cost-benefit equations. For example, humans may choose to engage in an activity for the cognitive stimulation or fun of it, even when there are potentially high short-term costs, accounted for by an awareness of long-term consequences (Berlyne 1966). This study does not account for some of the non-caloric benefits which honey-hunters may seek (e.g., enjoyment of the activity, or possible increases in social status via access to a highly sought-after food item). Similar considerations and issues have been raised in the study of cost-benefit dynamics in the human–dolphin mutualism (Cantor et al. 2018).

Additionally, opportunity costs have not been clearly outlined and calculated in this chapter. The benefits of cooperating with honeyguides could be modelled in a similar way to that of the commensal use of domestic dogs for hunting in Nicaragua. Koster (2008) used an optimal foraging model to show that Nicaraguan hunters in forest habitats increased their chances of harvesting preferred prey by hunting with dogs, despite the added cost of dogs occasionally chasing less profitable prey. Our dataset on honeyguides offers an opportunity to model the human-animal system in Niassa using a similar approach.

Conclusions

This study found that honeyguides are located in any part of the Niassa landscape with wild bees' nests. Honeyguides successfully guided humans to bees' nests in a direct trajectories on the majority of occasions, demonstrating that they know where bees' nests are located. Honeyguides also successfully guided honey-hunters to bees' nests more often than they failed. Honeyguides were measurably useful partners because they significantly increased the rate at which bees' nests were found and reduced the search distance per bees' nest compared to bees' nests that humans found on their own, and because the number of honeyguides successfully encountered in a day of honey-hunting strongly predicted the quantity of honey harvested. There was mutualistic asymmetry in rewards gained following harvests, but an outcome where both partners benefitted was the most common outcome. In this non-obligate, pseudo-reciprocal mutualism, failed interactions appeared to have a low cost to both partners. Future research could apply optimal foraging models to this system to better understand decision-making and opportunity costs for honey-hunters and honeyguides.



CHAPTER 3

When wax wanes: competitors for beeswax stabilize rather than jeopardize the honeyguide–human mutualism

Abstract

Many mutualisms are exploited by third-party species, which benefit without providing anything in return. Exploitation can either destabilize or promote mutualisms, via mechanisms that are highly dependent on the ecological context. Here we study a remarkable bird–human mutualism, in which wax-eating greater honeyguides (*Indicator indicator*) guide humans (*Homo sapiens*) to wild bees' nests, in an exchange of knowledge about the location of nests for access to the wax combs inside. We test whether the depletion of wax by mammalian and avian exploiter species either threatens or stabilizes the mutualism. Using camera traps, we monitored feeding visits to wax comb made available following honey harvests. We found that greater honeyguides face competition for wax from conspecifics and nine exploiter species, five of which were not previously known to consume wax. Our results support the hypothesis that heterospecific exploiters stabilize the mutualism, because wax depletion by these competitors probably limits feeding opportunities for conspecific exploiters, favouring the early-arriving individual that guided humans to the bees' nest. These findings highlight the importance of the ecological

context of species interactions and provide further evidence for how mutualisms can persist because of, and not in spite of, exploitation by third-party species.

Introduction

Mutualisms between species are an influential element of ecological food-webs and have played an important role in the diversification and coexistence of life (Chomicki et al. 2020; Mougi and Kondoh 2012; Weber and Agrawal 2014; Weiblen and Treiber 2015). Species which form mutualistic partnerships are directly and indirectly affected by other species within their ecological community (Palmer et al. 2015), and competition towards mutualists by third-party species is often highly influential in shaping the ecology and dynamics of mutualisms (Bronstein 2001; Chamberlain et al. 2014; Jones et al. 2012. Exploitation by non-mutualists should destabilize mutualisms, or even drive one of the partners extinct through competitive exclusion (Ferriere et al. 2002; Sachs and Simms 2006). Nonetheless, many mutualisms persist or even thrive despite exploitative behaviour, potentially due to wide variation in the costs placed on mutualists by exploiters, and the specific defensive mechanisms which have evolved against exploitation (Chomicki et al. 2020; Frederickson 2017; Kiers et al. 2011).

Although many mutualisms have been well studied under controlled or isolated *ex situ* conditions (e.g. between plants and mycorrhizae; Kiers et al. 2011), to better understand the selective forces and evolutionary stability of some mutualisms, it can be informative to study mutualistic partners and their competitors in their natural ecological setting (Chomicki et al. 2020; Jones et al. 2012). This is because the mechanisms by which mutualisms are resilient to exploitation from non-mutualists are highly diverse (Chomicki et al. 2020) and are often strongly related to both the specifics of the mutualism and to the ecological context in which they evolved (i.e. the sum of direct and indirect interactions between mutualists and their competitors, over a range of spatial and temporal scales) (Chomicki et al. 2020; Frederickson 2017; Hoeksema and Bruna 2015). Furthermore, stabilizing mechanisms against exploitation are commonly affected by the level of dependence between mutualistic partners, and in particular whether the mutualism is obligate or facultative (Chomicki et al. 2020). This further reinforces the value of studying mutualisms within the environment in which they evolved.

Here we studied a remarkable mutualism between humans and a wild bird species, the greater honeyguide (*Indicator indicator*), to map a guild of exploiter species, quantify the impact of these exploiters on the rewards available to mutualists, and investigate the likely consequences of these impacts for the stability of the mutualism. Greater honeyguides and humans are facultative partners in a reciprocal foraging mutualism (Connor 1995; Isack and Reyer 1989), in which a greater honeyguide leads human honey-hunters to wild bees' nests (primarily honeybees of the subspecies *Apis mellifera scutellata*) using vocal signals supplemented by visual cues (Isack 1987; Short and Horne 2001; Spottiswoode et al. 2016; Wood et al. 2014). The birds benefit from eating the beeswax left behind after the humans harvest the honey (typically using an axe to access the nest and smoke to subdue the bees) (Diamond and Place, 1988; Isack and Reyer, 1989, and the humans benefit from information about where hidden bees' nests are located, and so from the calorific richness of honey and bee eggs, larvae and pupae (hereafter 'bee larvae') (Short and Horne 2001; Spottiswoode et al. 2016). In common with other cases of human–wildlife cooperation (Cram et al. 2022), each partner both provides and receives a service (guiding to the bees' nest by the greater honeyguide, harvest of bee products by the human) and a resource (wax for the bird, honey for the human).

It has long been implicitly assumed that the human–honeyguide mutualism is stable (where it remains a frequent part of human foraging) because wax is a highly specialized food resource eaten by only a few species (Friedmann and Kern, 1956; Hepburn, 2009; Obst, 1986; Place and Stiles, 1992; Schmidt-Nielsen, 1997), such that greater honeyguides have essentially exclusive feeding access once it has been made accessible within the environment (Friedmann and Kern, 1956). However, if other species do consume the wax, potentially attracted by conspicuous visual and acoustic cues while humans harvest a bees' nest, and olfactory cues following the harvest, it could affect the human–honeyguide mutualism in two ways. First, competition for wax could reduce or abolish the reward to the greater honeyguide that invested time and energy in guiding the human, thus disincentivizing guiding behaviour and destabilizing the mutualism. Alternatively, increased competition may strengthen the mutualism by depriving other greater honeyguides (which did not guide the human) of opportunities to scrounge on the wax, thus increasing the marginal benefits to the guiding bird. Within nutritional mutualisms, in which one species provides its mutualistic partner with a resource or behavioural service (e.g. pollen transport between flowers) in exchange for a reward (e.g. nectar), the influence of competitors is often particularly apparent (Bronstein, 2001b; Jones et al. 2012). This is because it is relatively easy to detect the food being consumed by non-mutualists who have not incurred the costs of its production (Palmer et al. 2015).

In this study, we used camera traps at natural honey-harvest sites to investigate beeswax depletion both by greater honeyguides and by heterospecific competitors. We first demonstrate the surprising level of competition that greater honeyguides face for a specialized resource, showing that a range of taxa previously unknown to eat wax, in fact regularly do so. Next, we test the predictions of two hypotheses regarding how this unexpected competition may influence the stability of the human–honeyguide mutualism. Our first hypothesis is that competition could *destabilize* the mutualism by reducing the benefits to the greater honeyguide of guiding behaviour. This hypothesis predicts that (i) competitors deplete the wax before greater honeyguides are able to feed, such that honeyguides do not obtain consistent feeding opportunities. This effect would be greatest if (ii) the most important competitors are diurnal and (iii) competitors consistently displace greater honeyguides from a wax resource. Our second hypothesis is that if honeyguides still get feeding opportunities despite heterospecific competition, then heterospecific competitors may, counterintuitively, *stabilize* the mutualism against conspecific competitors by decreasing the returns of arriving late at the resource, and therefore favour individual greater honeyguides that cooperate with humans. Specifically, this hypothesis predicts that (i) greater honeyguides should be first-arriving species after the wax has been exposed; (ii) the majority of greater honeyguide feeding events should be before other species feed (that is, that honeyguide feeding events should diminish after heterospecific competitors arrive) and (iii) late-arriving greater honeyguides miss feeding opportunities, because (iv) visits by heterospecific competitors fully deplete the wax.

Material and methods

Study site

We carried out this study in a 28 km^2 area within the Niassa Special Reserve in northern Mozambique (see also Chapter 1 and 2). Our study area is in range of Yao honey-hunters' foraging trips from Mbamba village (12°12′S, 38°01′E; *ca* 2,000 inhabitants including > 30 regular honey-hunters). Yao honey-hunters traditionally reward greater honeyguides after a successful honey harvest by leaving a small pile of beeswax near the harvested bees’ nest (Figure 3.1), and therefore the main source of wax for greater honeyguides in this landscape is that left behind or exposed by humans at the harvest site of a bees' nest (Spottiswoode et al. 2016). Within this area, the costs and benefits of the human–honeyguide mutualism appear to approximate those under which it presumably evolved: there is little apiculture and a minimal cash economy for buying sugar instead of honey (Spottiswoode et. al., 2016). The climate is sub-humid tropical with mean minimum and maximum air temperatures ranging between 16–33°C in the dry season (May–October) and 22–32°C in the wet season (November–April). Rainfall begins in November and ends in late April or early May; during this period, precipitation averages 250–350 mm per month. Bees' honey stores, which build up throughout the rains with the flowering of dominant species, peak in May–June, deplete as the dry season progresses and then peak again in November–December following the flowering of trees prior to the following rainy season (Lawton, 1982). Data were collected from 24 September to 25 October 2015, 29 August to 15 October 2017, 4 November 2018, and 24 September 2021 to 7 October 2021.

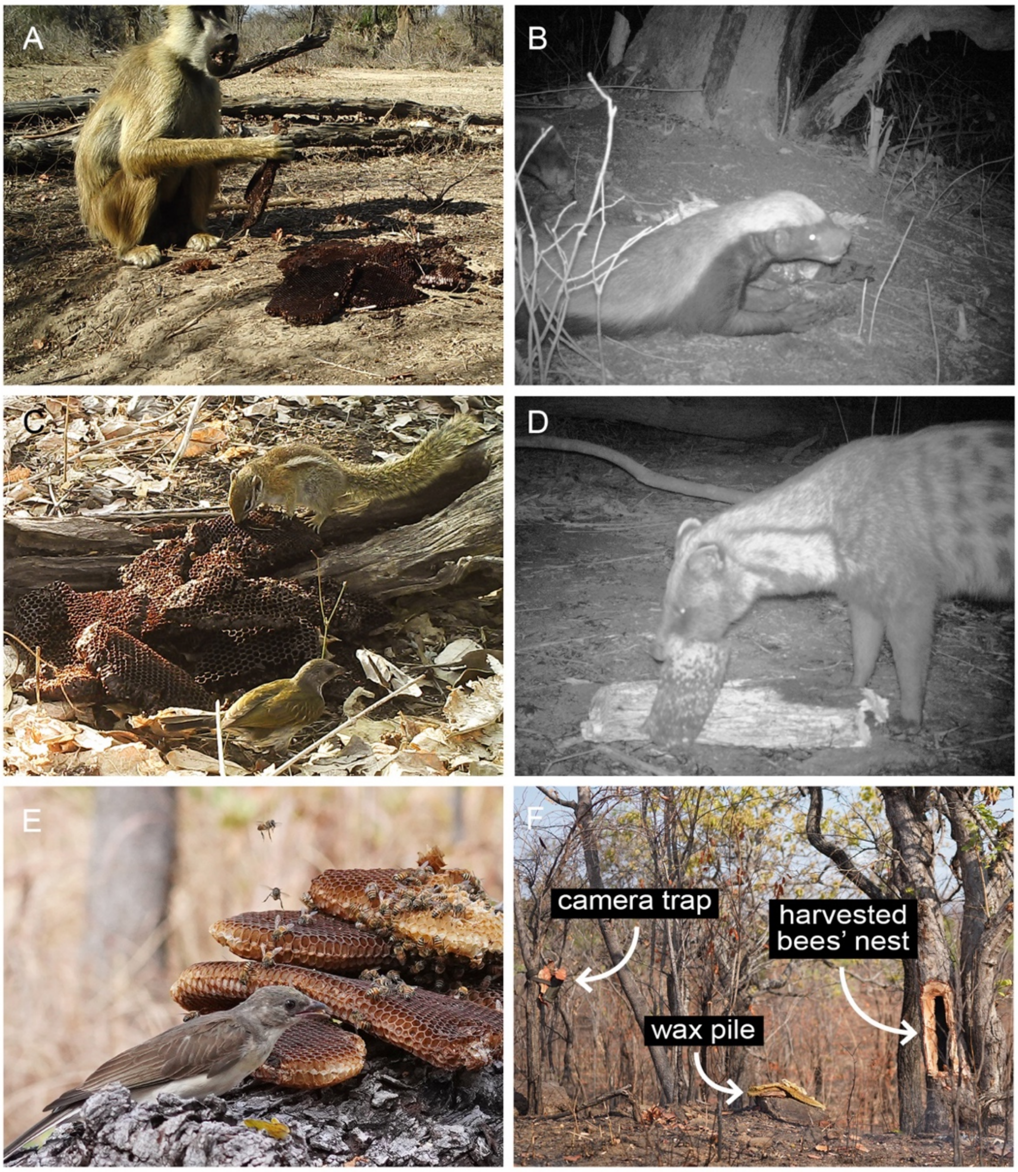


Figure 3.1. (A-F) Humans leave wax comb as a reward to greater honeyguides after a honey harvest, and this is eaten by birds and mammals. (A) Yellow baboon (*Papio cynocephalus*) during the day and (B) honey badger (*Mellivora capensis*) at night are two of the major competitors for wax which greater honeyguides (*Indicator indicator*) face. Other wax-eating animals with a lesser impact on wax availability include (C) striped bush squirrel (*Paraxerus flavovittis*) and scaly-throated honeyguide (*Indicator variegatus*), and (D) African civet (*Civettictis civetta*); (*a–d*) show camera trap images collected during the study. (E) An early-arriving female greater honeyguide (*Indicator indicator*) feeds on wax prior it being depleted. (F) Photograph showing the positioning of a camera trap relative to a pile of wax and a harvested bees' nest.

Honey harvests, wax and camera trap placement

Wax-eating data were collected at 26 small piles of wax comb (approx. 0.1–1.5 kg) placed on the ground or a horizontal tree log, in a manner reflecting the honeyguide rewarding culture displayed by Yao honey-hunters (Figure 3.1). These were located at 26 bees' nests (six nests in 2015, four in 2017 and 16 in 2021) which were found during honey-hunts conducted in a traditional manner. Eleven sites where camera traps were placed from 2015 and 2017 were excluded from the analysis either due to camera trap malfunction or because the wax was left without harvesting the bees’ nest. To initially locate the bees' nests, one or two researchers (David Lloyd-Jones, Claire Spottiswoode and James St Clair) accompanied two Yao honey-hunters (one of whom was a main assistant and is a co-author: Orlando Yassene) on a honey-hunt as they elicited guiding behaviour from greater honeyguides using stereotypical calls (Spottiswoode et al. 2016). Twenty-two of the 26 nests were located by guiding from a greater honeyguide, two were located opportunistically prior to being guided while walking in the same habitat and two were found in the same habitat after unsuccessful guiding by a greater honeyguide. All bees’ nest locations were previously unknown to us or the honey-hunters prior to the study, and at all 26 sites honey and wax were extracted by two honey-hunters using traditional methods (smoke and axes). The honey-hunters retained the combs containing honey and left behind a pile of wax combs without honey: these included a mixture of wax types, including smaller pieces of newly produced, empty white wax comb (most favoured by greater honeyguides), older wax comb with bee larvae in it, and dark wax comb containing old larval casings and no larvae (least favoured by greater honeyguides; David Lloyd-Jones, James St Clair, Dominic Cram, Orlando Yassene, Jessica van der Wal, Claire Spottiswoode, personal observation; see also Isack (1987). In all cases, the wax piles were consistent with those that Yao honey-hunters naturally leave as reward following a successful harvest at a bees' nest they were guided to by a greater honeyguide.

To record animals eating visiting wax combs during the day and night, a camera trap (Acorn 6210, Ltl Acorn, Denmark, Wisconsin) was set up for 1–9 days at each site (total = 88.8 trap days; mean ± SE duration per site = 3.41 ± 0.39 days) at a height of 80–90 cm above ground and 1.5–2 m from the wax pile, facing slightly downwards (26.6 trap days in 2015, 15.7 trap days in 2017, 46.5 trap days in 2021). Each camera trap was set to trigger with a 5 s delay and take photos at 10 s intervals for as long as the camera was motion triggered. The cameras also recorded a video clip of 10 s or 30 s, alternating with sets of three photos for as long as the camera was motion triggered. Coordinates of the bees' nest were marked with GPS (Garmin eTrex 30, Garmin USA) and all camera traps checked every 1–2 days.

For each animal detected, the duration of wax-feeding events was estimated from image and video clip time stamps. Feeding events were defined as contact between the mouth or bill of the animal and any part of the wax comb pile. Whenever possible we recorded which food type was eaten (wax only, larvae only, or wax and larvae together), but due to the resolution of the images we were not able to reliably score which type of wax was eaten by each animal. Short feeding events, such as when the animal disappeared prior to a second image being taken, and therefore without a reliable 'end time', were recorded as having a 2 s duration. At one wax site, feeding greater honeyguides disappeared to feed inside the log from which the honey and wax were harvested, and were observed emerging with small pieces of white wax. For these few observations (5 of 39 visits at this site), the period that the bird was out of view was recorded as feeding time.

Statistical analysis

All statistical analyses were carried out using R v. 4.0.3 (R Core Team, 2020). To document the level of competition that greater honeyguides face for beeswax, we summarized the following for each wax placement site (n = 26): number of wax-eating visits by each species, first-arriving species and species which ate the last remaining wax (where known). Feeding times for all wax-eating species were plotted over 24 h and compared to median sunrise and sunset times (generated using the *suncalc* package; Thieurmel and Elmarhraoui, 2019) for our study duration.

To test prediction (i) of hypothesis one (*competitors deplete the wax before greater honeyguides feed*), we calculated the proportion of sites at which greater honeyguides fed, the frequency of feeding visits per hour and the proportion of visits which resulted in the wax pile being depleted for each species. Then, using data for the eight most frequent wax-eating species (defined as those with > 5 visits: greater honeyguide; scaly-throated honeyguide, *Indicator variegatus*; lesser honeyguide, *Indicator minor*; striped bush squirrel, *Paraxerus flavovittis*; African civet, *Civettictis civetta*; honey badger, *Mellivora capensis*; yellow baboon, *Papio cynocephalus*; Meller's mongoose, *Rhynchogale melleri*), we fitted a univariate Cox's proportional hazards survival model for arrival at wax (the event) for greater honeyguides and the other seven competitor species (pooled) using the *survival* package (Therneau, 2020). The response term was time since wax placement, and a binary variable denoting whether the final visit time was unknown (right-censored events). The proportional hazards assumptions of this Cox regression model were met (checked by visual inspection of proportional hazard plots and tested using the 'cox.zph' function in the *survival* package; all $p > 0.05$). The results are presented as hazard ratios (HR) with corresponding 95% confidence intervals (CI).

To test prediction (ii) of hypothesis one (*most important competitors are diurnal*), we tallied the number of visits of species which consumed wax, and the time of day at which depletion (time when final piece of wax is consumed) occurred. To test prediction (iii) of hypothesis one (*diurnal competitors consistently displace greater honeyguides from a wax resource*), we first calculated the proportion of visits by diurnal competitors at wax (scaly-throated honeyguides, lesser honeyguides, striped bush squirrels, yellow baboon and slender mongoose, *Herpestes sanguineus*) which were simultaneous with greater honeyguides, then calculated the proportion of greater honeyguide feeding visits which were cut short by either of these five competitor species, and the number of greater honeyguide visits which were immediately before or after competitor species (within 10 s).

To test prediction (i) of hypothesis two (*greater honeyguides are the first-arriving species after the wax has been exposed*), we calculated the proportion of sites where greater honeyguides arrived first, along with the previous Cox's proportional hazards survival model of arrival at wax by greater honeyguides and competitor species. To test prediction (ii) of hypothesis two (*the majority of greater honeyguide feeding events occur before major wax competitors*), we first observed that the larger bodied mammals (greater than 1 kg) appearing in the images were honey badger, yellow baboon, Meller's mongoose and African civet.

Preliminary observations suggested that although civets frequently visited wax sites, they were messy and often left substantial wax available, only depleting all available wax at 2 of 26 sites. For this analysis, we therefore defined the major wax competitors as yellow baboon, honey badger and Meller's mongoose, and counted the number of greater honeyguide visits to wax that occurred before or after the visits of these species, and also the number of greater honeyguide visits spent looking for pieces of wax after the wax was depleted. These counts were fitted as the response term in a generalized linear mixed effects model (GzLM) with a Poisson distribution. The number of camera trap days for each interval was included as an offset to account for variation in sampling effort, and wax placement site was included as a random term in addition to an observation level random to account for overdispersion. Similarly, we compared the feeding durations of greater honeyguides before and after the arrival of major wax competitors using a GzLM with a Gamma distribution (selected due to the data having positively skewed errors) with time spent feeding as the response term and visit interval (before major wax competitors, after major wax competitors, after wax depletion) as the predictor, and wax placement site as the random term. For both models, we report chi-squared statistics of an analysis of variance between the model of interest and the null model. Assumptions of normality for both GzLMs were assessed by visual inspection of the distribution of residuals. Effect sizes (estimated marginal means) were calculated using the *emmeans* package (Lenth et al. 2022). Feeding rates for greater honeyguides were calculated by dividing the total number of feeding visits by the total number of daylight hours the wax was available for (daylength was calculated using the *suncal* package (Thieurmel and Elmarhraoui, 2019), over all sites. This was repeated for visits before and after major wax competitors.

We tested prediction (iii) of hypothesis two (*late-arriving greater honeyguides miss feeding opportunities*) by comparing the duration of greater honeyguide feeding visits to wax before and after major wax competitors arrived using the same GzLMs as for prediction (ii) of hypothesis two. We tested prediction (iv) of hypothesis two (*visits by heterospecific competitors fully deplete the wax*) using a Cox's proportional hazards model of wax survival with the arrival of major wax competitors (yellow baboon, Meller's mongoose and honey badger) as a time-dependant covariate. The response terms were the time until depletion after wax placement and arrival times of major wax competitors, and we included right-censored data as a binary variable (sites where the time of final wax depletion was unknown). The proportional hazards assumptions of this Cox regression model were checked as above and results presented as HR with corresponding 95% CI.

Results

Greater honeyguides experience surprising competition for wax from heterospecifics

We found that 10 vertebrate species consumed beeswax (four birds, including greater honeyguides, and six mammals; Figure 3.2). All but one species was recorded on our camera traps, yielding 1098 unique wax-eating visits. A crowned hornbill (*Tockus alboterminatus*) was observed eating wax comb (beeswax and larvae together) at a separate honey harvest in November 2018 where no camera trap was placed.

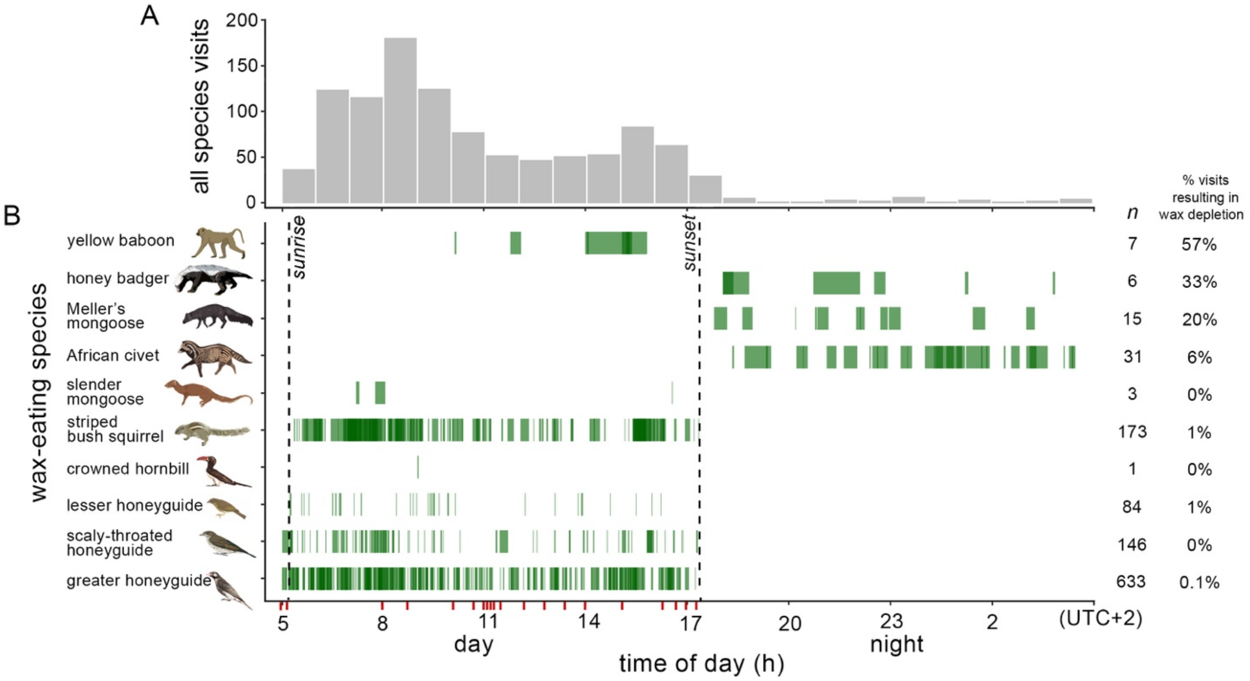


Figure 3.2. Ten species were recorded eating wax yet differed in the time of day they fed and in feeding duration, and we observed a clear day–night difference in feeding visits. (A) Frequency of feeding visits by hour of day—each vertical bar corresponds to the total number of visits recorded within that hour; this is grouped for all days that wax was available at 26 wax sites and includes revisits by a single individual. (B) Green horizontal bars represent the time of day and feeding duration of visits detected at piles of wax comb and are plotted with 50% transparency such that events occurring at the same time of day appear darker. Dashed vertical lines represent the median sunrise and sunset time during the data collection periods. Red tick marks along the x-axis represent the wax placement times (i.e. when the wax was first available to be eaten). Total number of observed visits for each species are listed on the right (*n*). Percentage of visits for each species' which resulted in total wax depletion is listed to far right.

Wax-eating species differed markedly in the time of day when they fed (Figure 3.2A). Four bird species (greater honeyguide, lesser honeyguide, scaly-throated honeyguide and crowned hornbill) and three mammal species (striped bush squirrel, slender mongoose and yellow baboon) were observed feeding only during daylight hours, from a median sunrise of 05:15 to median sunset of 17:25. Three larger bodied mammal species (honey badgers, African civets and Meller's mongoose) were only observed feeding on wax at night (Figure 3.2B). For five species (striped bush squirrel, slender mongoose, Meller's mongoose, yellow baboon and crowned hornbill), these are the first records, to our knowledge, of wax-eating behaviour (Kingdon 2014). Overall, a mean ± SE of 4.14 ± 0.32 (median = 4, range = 1–7) wax-eating species visited each wax site (see Appendix to Chapter 3). Three major wax-depleting species (yellow baboon, honey badger and Meller's mongoose) were responsible for 11 out of 20 (55%) observed wax depletions (where the final animal to finish the wax was known). When these ‘major wax competitors' fed at a wax site, the probability of all the wax being entirely depleted on that specific visit was 32%. Three mammalian wax-eating competitors (honey badger, African civet and Meller's mongoose) only fed on wax nocturnally, despite wax always becoming available diurnally (Figure 3.2B). Honey badgers arrived and fed at 4/26 sites (15%), Meller's mongoose fed at 7/26 wax sites (27%) and civets arrived and fed at 12/26 wax sites (46%). These three species finished all available wax on 33%, 20% and 6% of visits, respectively. The overall proportion of wax placements depleted by sunrise on day two was 12%, and by sunrise on day three was 46%.

During the day, yellow baboons and striped bush squirrels were the primary competitors for wax, but in different ways. Yellow baboons only arrived at 7/26 wax sites (27%) yet ate all available wax on 4/7 occasions (57%) and fed for considerable periods of time (mean ± SE of 1375 ± 128 s) while taking the time to dextrously pick up even minute pieces of wax, thus depriving later greater honeyguides of feeding opportunities. By contrast, striped bush squirrels made numerous visits to known wax sites (Figure 3.2B, mean visits per site ± SE of 14.4 ± 2.9) and fed for considerable periods of time (mean ± SE of 293 ± 42 s) per visit. Striped bush squirrels totally depleted 2 of 20 wax sites where the final animal to feed was known (10%), yet unlike all the larger bodied competitors, did so without physically excluding greater honeyguides from access to wax.

Does competition by heterospecifics destabilize the mutualism?

The first prediction of hypothesis one is that *competitors deplete the wax before greater honeyguides are able to feed*. Instead, we found that greater honeyguides were significantly more likely to arrive at wax earlier than their seven main wax-eating competitors (Figure 3.3A; Cox model: HR = 4.85 [95% CI = 3.30, 7.12], Z = 8.04, $p < 0.001$). We observed that greater honeyguides were the first species to feed at 18 of 26 sites (69%) and successfully fed on wax at 23 of 26 wax sites (88%). Even when bees were located without the help of a greater honeyguide, this species was still the first to feed on the wax at three of four sites (75%).

The second prediction of hypothesis one is that the *most important competitors are diurnal.* Of the 20 sites at which we observed an animal depleting the wax, diurnal species depleted 65% of sites, while nocturnal species depleted 35% of sites. The key diurnal species were yellow baboon (depleting 20% of sites) and bush squirrel (depleting 10%), while the nocturnal species were Meller's mongoose (depleting 15% of sites) and honey badger (depleting 10% of sites). Importantly, when diurnal species depleted the wax, they did so on the first day at only 10% of sites, and thus even if a diurnal species depleted the wax, greater honeyguides would typically still have opportunities to feed.

The third prediction of hypothesis one is that *competitors consistently displace greater honeyguides from a wax resource*. Instead, we found that the interaction of greater honeyguides with other species at wax was relatively uncommon. It occurred primarily with scaly-throated honeyguides, which both chase and are chased away from wax by greater honeyguides (personal observation; Downs et al. 2002). Lesser honeyguides were three times observed being chased away from wax by greater honeyguides, whereas striped bush squirrels were observed feeding alongside greater honeyguides 17 times with minimal agonistic behaviour. Greater honeyguide feeding visits were visibly cut short only once out of 633 feeding visits (less than 1%; by a scaly-throated honeyguide), and greater honeyguides fed simultaneously to squirrels (n = 17), lesser honeyguides (n = 11) and scaly-throated honeyguides (n = 22) on 50 out of 633 feeding visits (7.8%). Greater honeyguides fed immediately before or after one of these three species on 24 out of 633 visits (3.7%), indicating that while competitive displacement from wax can occur, exclusion is not widespread, and its effects are limited.

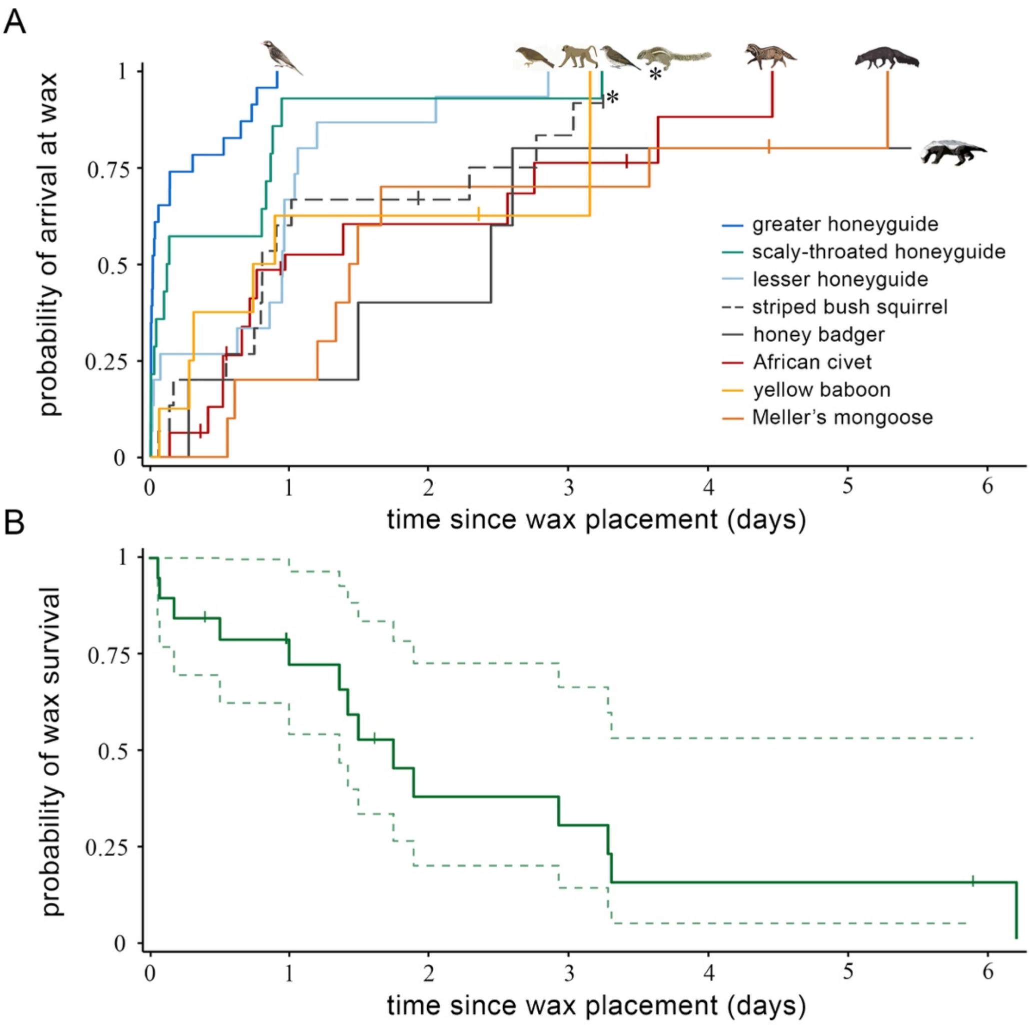


Figure 3.3. Beeswax rapidly disappears when left at a honey-harvest site, due to the arrival of wax-eating mammals, yet greater honeyguides consistently arrive at wax ahead of competitor species. (A) Lines show the probability of arrival and wax-eating by one of the seven most common wax-eating species. These inverse Kaplan–Meier survival curves approximate the cumulative probability that a species will arrive at wax by a given time, given that they arrive at all. Steeper slopes indicate that a species, in general, finds the wax resource more quickly after it becomes exposed. Crosses mark censorship events, which are visits after the wax was depleted. (B) Solid green line indicates the Kaplan–Meier survival function of beeswax comb in its natural setting. Dashed pale green lines represent model predictions with 95% CIs. Crosses indicate censorship events which are sites where the times of final wax depletion were unknown.

Honey badgers, civet, yellow baboon and slender mongoose all are considerably larger than honeyguides and are opportunistic bird predators (van der Wal et al. 2022b), so would be expected to displace greater honeyguides at wax. Instead, we found that honey badgers and civets fed on wax entirely nocturnally and thus were not observed interacting with greater honeyguides (Figure 3.2). Diurnal slender mongooses tended to arrive later to wax sites than greater honeyguides (Figure 3.3A) and were less likely to arrive at wax overall: they appeared on the camera traps at 5 of 26 (19%) of wax sites but only arrived before wax depletion at 2 of 26 (7.6%) sites. Therefore, these four possible predators appear to have a minimal influence on greater honeyguides' direct access to available wax, but rather deplete the wax resource at times when greater honeyguides never or rarely visit.

Could competition by heterospecifics stabilize the mutualism against conspecific exploiters?

If greater honeyguides obtain feeding opportunities despite heterospecific competition, then heterospecific competitors may, counterintuitively, stabilize the mutualism against late-arriving conspecific exploiters (i.e., greater honeyguides that have not participated in the mutualism by guiding the human) by depriving them of wax. Hypothesis two makes four predictions, which we test using our data. First, *greater honeyguides are the first-arriving species after the wax has been exposed*. Our data provided strong support for this prediction, because greater honeyguides were the first wax-feeding species at 69% of sites (n = 18), and overall, they discovered wax earlier than all other species (Figure 3.3A), with 56% of wax-eating visits falling within the first 24 h after wax availability.

Second, hypothesis two predicts that *the majority of greater honeyguide feeding events occur before major wax competitors*. Our data strongly supported this prediction. We found that greater honeyguides visited wax significantly more often before the arrival of major wax competitors (yellow baboon, honey badger and Meller's mongoose) than after major wax eaters arrived, but before all wax was depleted (GzLM: $\chi2$ = 250, d.f. = 2, $p < 0.01$, n = 45 counts; Figure 3.4A). Number of greater honeyguides visits reduced by 89.5% after major wax competitors arrived, compared to before their arrival (0.74 ± 0.15; effect size ± SE from GzLM; Figure 3.4A). Additionally, greater honeyguide feeding rates (number of feeding visits per hour of daytime that wax was available) reduced from an average of 0.92 visits per hour to an average of 0.74 visits per hour (19.6% reduction).

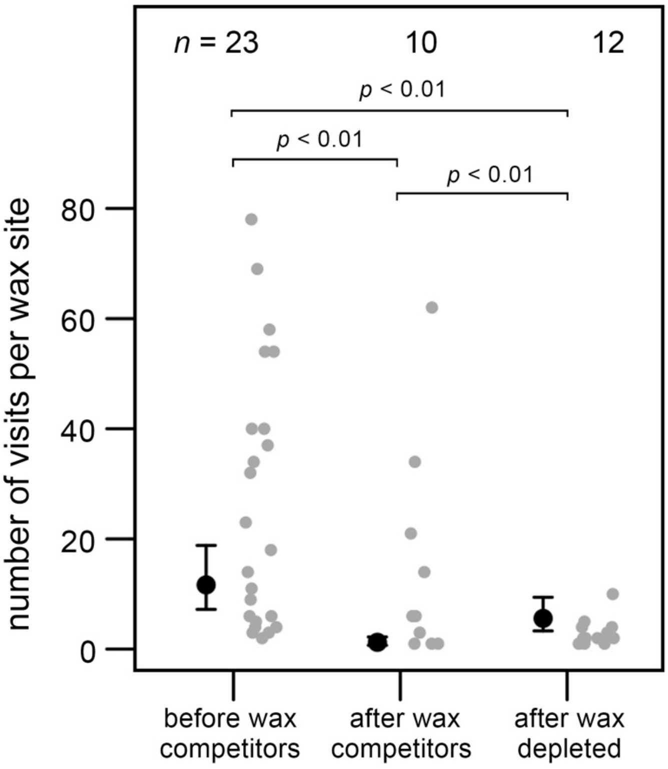


Figure 3.4. Greater honeyguides visited wax significantly more prior to the arrival of major wax competitors (yellow baboon, honey badger and Meller's mongoose) than afterwards. After all wax was depleted, greater honeyguides made more visits to search for wax than they had done when wax was still available. Black points and error bars show the predicted means and standard errors from a generalized linear mixed effects model which accounts for variability in sampling duration (i.e. how long wax was available for at each site). Grey points show the raw data.

Third, hypothesis two predicts that *late-arriving greater honeyguides miss feeding opportunities*. Our data provided mixed support for this prediction. Importantly, as detailed above, greater honeyguides made fewer visits to the wax after it had been visited by a major wax competitor, supporting this prediction. However, greater honeyguides that visited the wax after major wax competitors did not, as predicted, rapidly leave the site because they found no wax remaining, and instead appeared to spend longer looking for small wax pieces as well as picking apart wax comb with more larval casings and of lower wax content. Consequently, we did not find that greater honeyguides fed at or visited the wax site for significantly less time after the arrival of wax-depleting species (GzLM: $\chi2 = 1.65$, d.f. = 2, p = 0.43, *n* = 783).

Finally, and critically, hypothesis two predicts that *visits by heterospecific competitors fully deplete the wax*. This prediction was strongly supported. We found that collectively, visits by the three major wax competitors (yellow baboon, Meller's mongoose and honey badger), were significantly associated in time with the complete depletion of wax (Figure 3.3B: HR = 5.04 [2.11, 12.0], $Z = 3.64$, $p < 0.01$). This result is non-significant when visits by civets are included in the predictor variable, as expected since civets are not major wax competitors because they feed messily and rarely deplete the wax (Methods). The likelihood of all wax being depleted (Figure 3.3B) across all sites was 19% (95% CI = 3–33%) at 24 h after it became available, 53% (95% CI = 28–70%) at 48 h and 58% (95% CI = 32–74%) at 72 h.

Discussion

Our results suggest that the observed persistence of the human–honeyguide mutualistic foraging partnership may be at least partly *due to,* and not *in spite of*, heterospecific consumption of the wax reward it produces. Prior to our results, the implicit assumption has been that greater honeyguides have essentially unrestricted feeding access to wax once it is made accessible, because few other species can digest it, such that this monopoly on wax-eating maintains the human–honeyguide mutualism. Our findings overturn these assumptions because greater honeyguides face stiff competition for wax from a surprising range of taxa, including some previously not known to eat wax. Despite this unexpected heterospecific competition for wax, our data were most consistent with the hypothesis that this competition stabilizes the mutualism against conspecific exploiters (Table 3.1), by reducing the benefits of arriving late at the resource (and therefore favouring, at each site, the early-arriving individual greater honeyguide that cooperated with humans). This was supported by the relatively rapid removal of wax by heterospecific competitors after it first became available, and by a consequent reduction in feeding by late-arriving greater honeyguides.

Conversely, we did not find support for the hypothesis that heterospecific competition for wax destabilizes the mutualism. Greater honeyguides were frequently able to feed on wax prior to and after other species' arrivals and even when temporarily displaced by other animals. At piles of wax not found in the daytime by yellow baboons, the two species which most consistently finished all the wax upon arrival (Meller's mongoose and honey badger) were only observed to eat wax nocturnally, therefore allowing a daytime period after a honey harvest during which greater honeyguides have opportunities to feed. Anecdotally, we also observed greater honeyguides flying away from the wax piles with large pieces of new, white wax comb, potentially to cache them (Isack 1987; Short and Horne 2001). Caching behaviour by early-arriving greater honeyguides would provide them with *ad libitum* wax for several days, while late-arriving individuals are deprived (by the early birds, and other competitors) of the new white wax which they prefer (David Lloyd-Jones, Orlando Yassene, Claire Spottiswoode: 2015, 2017, 2018, personal observation; Diamond and Place 1988).

Table 3.1. Competition for beeswax exposed by the human–honeyguide mutualism may play an unrecognized role in the mutualism's ecological dynamics and evolutionary stability. Our data were most consistent with the hypothesis that competition by heterospecifics stabilizes the mutualism against conspecific exploiters, by increasing the benefits to honeyguides of arriving early at the resource.

Hypothesis 1: Competition for wax *destabilises* the mutualism by reducing the benefits to the honeyguide from guiding behaviour	**Support?**
Predictions	
(i) competitors deplete the wax before honeyguides are able to feed	**no**
(ii) the most important competitors are diurnal	**mixed**
(ii) competitors consistently displace honeyguides from a wax resource	**no**
Hypothesis 2: Heterospecific competitors *stabilise* the honeyguide-human mutualism against conspecific exploiters by decreasing the returns of arriving late at the wax resource	
Predictions	
(i) greater honeyguides are first-arriving species after wax has been exposed	**yes**
(ii) the majority of greater honeyguide feeding events are before other species feed (i.e. honeyguide feeding events diminish after heterospecific competitors arrive)	**yes**
(iii) late-arriving greater honeyguides miss feeding opportunities	**mixed**
(iv) visits by heterospecific competitors fully deplete the wax	**yes**

competitors destabilise mutualism

↕

competitors stabilise mutualism

Our findings that greater honeyguides are typically the first species to arrive at wax, and that more than one individual arrived and fed at every site which this species visited, indicate that intraspecific dynamics are also relevant to the mutualism's stability. For example, these observations raise the question of why greater honeyguides guide humans when they can readily exploit the guiding efforts of other greater honeyguides. Answering this requires further investigation into the benefits of guiding and wax-eating at the individual level. Additionally, the interactions between greater honeyguides and scaly-throated honeyguides need further investigation; these two species are similar in size and mass (greater honeyguides in Niassa: mean mass 47.7 g, range 59.5–35.5 g, $n = 124$; scaly-throated honeyguides in Niassa: mean mass 48.1 g, range 54.5–40.5 g, $n = 26$), and do not appear capable of entirely excluding each other from wax, even when four scaly-throated honeyguides were present at the same time as one greater honeyguide (personal observation). The probability of scaly-throated honeyguides finding wax within the first few hours after it became available is initially very similar to that of greater honeyguides (Figure 3.3A), but rapidly reduces as time passes. This suggests that competitors may eavesdrop on the guiding signals from greater honeyguides to humans, as well as on the cues of a honey harvest including chopping sounds, smoke and increased bee activity.

Our results indicate that the wax liberated by the human–honeyguide mutualism has a larger ecological impact than expected. Specifically, we provide evidence this wax provides a nutritional resource for a formerly unrecognized guild of nine species, and that wax-eating by these species was remarkably common: wax at honey-harvest sites fed on average 2.7 species other than greater honeyguides. Five of the six mammalian competitor species (all but yellow baboons) readily ate empty wax combs comprised newly deposited wax. This suggests that these species may have a means of gaining energy from wax digestion, and that the competition for wax towards greater honeyguides is not simply an incidental by-product of consumption of honey or bee larvae. Alternatively, white wax may indeed be indigestible for mammalian competitors, but be consumed because it smells like comb containing honey or larvae.

These findings have several ecological and conservation implications. First, our data add to the natural histories of the nine competitor species, in six of which wax-eating has not previously been documented. Our findings suggest that the physiological ability to digest wax may be much more widespread in terrestrial species than previously thought (Place and Stiles 1992). Second, our results reveal the influence of third-party species on a functioning mutualism involving our own species and highlight how mutualisms can exert substantial and potentially cryptic ecological effects. While the effects of the human–honeyguide mutualism on local honeybee, tree and wildfire ecology remain to be quantified, our findings uncover a guild of species that regularly benefits from wax released when humans and greater honeyguides cooperate. Third, our results may have conservation implications for the human–honeyguide mutualism because protecting it may require the conservation of major wax competitor species that help stabilize it. Reciprocally, the decline of the human–honeyguide mutualism would jeopardize not only the material and non-material benefits for the two species involved (van der Wal et al. 2022b), but may also have negative consequences for at least nine other wax-eating species.

Finally, these findings may help to explain why mutualism between greater honeyguides and humans persists across a diversity of human cultural traditions, regardless of whether or not the cooperating human culture actively rewards the guiding greater honeyguide. While the Yao honey-hunters at our study site in Mozambique consistently leave a pile of wax as a reward for the bird, other cultures (e.g. Boran (Isack 1987) and Awer (van der Wal et al. 2022a) people in Kenya, and Hadzabe, Sonjo, Maasai and Ndorobo people in Tanzania (Laltaika 2021; Wood et al. 2014) vary in how and when they leave a wax reward. Some honey-hunters attempt to deprive the honeyguide, reporting that hunger motivates the bird to immediately guide them to another bees' nest, and that the bird should only be rewarded—if at all—once they have harvested the day's final bees’ nest (Isack 1987; Laltaika 2021). In doing so, honey-hunting cultures which do not always actively leave a reward may favour early-arriving birds that can clean up whatever small scraps of wax remain, producing a similar effect to major mammalian wax competitors in this study. Thus, rewarding traditions which limit wax availability may stabilize the mutualism by a different mechanism to the one that hunter-hunters envisage.

It is well understood that most mutualisms influence and are influenced by non-mutualist taxa (Bastolla 2009; Chomicki et al. 2019; Ferriere et al. 2002). Exploiters or cheating species are common (Sachs and Simms 2006) and can remain closely associated with mutualisms over long spans of evolutionary time (Compton et al. 2010; Pellmyr and Leebens-Mack 1999; Pellmyr and Huth 1994). Given that the ecological guild of heterospecific competitors at our study site in the Niassa Special Reserve is probably not too dissimilar to those under which the honeyguide–human mutualism first evolved (Spottiswoode et al. 2016), it is plausible that similar competition has existed over much or all of its likely ancient evolutionary history (Cram et al. 2022), and so influenced its long-term maintenance.

Our findings align with recent work showing that in the cleaner–client interaction (a service-resource mutualism), the presence of third-party species directly influences the consistency (and thus stability) of the mutualism. Cleaning behaviour of brain coral by sharknose gobies (*Elacatinus evelynae*) was consistently more frequent when the presence of third-party species and mutualistic partner abundance locally increased (Dunkley 2020). Similarly, a third-party scale insect species was found to strengthen an ant–plant (resource–protection) mutualism which in turn stabilizes an entire African savannah ecosystem (Prior 2018). In the same ant–plant mutualism, the removal of an influential third-party mammal species caused mutualism breakdown (Palmer 2008). These studies, together with our work and recent theoretical advances (Stone 2020) collectively demonstrate the importance of third-party species to the stability of mutualisms via a range of mechanisms, including the creation of partner choice options (gobies and corals), elevation of marginal benefits to the mutualistic individuals (scale insects and ant–plant mutualism; honeyguides and humans), and increasing resilience to perturbations (Stone 2020).

Overall, our results show that an unexpectedly large number of species feed on the wax resulting from the human–honeyguide mutualism, and that instead of threatening the mutualism, this ecological community probably helps to stabilize it. Thus, the human–honeyguide mutualism both supports and is maintained by a community of wax-eating species. These findings provide further evidence for how mutualistic dynamics are often context-specific and yet remain stable despite heterospecific exploitation.

CHAPTER 4

To bees or not to bees: greater honeyguides sometimes guide humans to animals other than bees, but likely not as punishment

Abstract

Greater honeyguides (*Indicator indicator*) are well known to guide human honey hunters to wild bees' nests in exchange for beeswax as food. Centuries of African Indigenous accounts have intriguingly reported that honeyguides occasionally guide humans to animals other than bees, typically large animals dangerous to humans. This is interpreted by some human cultures as punishment for prior failure to reward the bird, and by others as an altruistic warning behaviour. Here, we present quantitative evidence from hundreds of honeyguide-human interactions in Mozambique of greater honeyguides guiding humans to snakes (n = 3) and a dead mammal (n = 1). We show that guiding behaviour to these vertebrates was (i) spatially and acoustically analogous to honeyguide behaviour when guiding to bees, (ii) did not occur more frequently after not being rewarded with beeswax by humans, and (iii) was rare (3.7% of human-honeyguide interactions in 1 year; 0% in others). We review historical accounts and cultural explanations for this behaviour and use these to inform five hypotheses for why honeyguides guide people to non-bee animals. Our field data were most consistent with the hypothesis that guiding to non-bee

animals results from a cognitive recall error of spatial information. We suggest that this behaviour is unlikely to function as punishment, yet may coincidentally benefit honeyguides over longer timescales by initiating a human cultural interpretation that reinforces human cultural traditions of rewarding honeyguides with beeswax.

Introduction

Mutualistic species partnerships are not always beneficial to both partners all the time (Bronstein 2001a). One partner may fail to provide the reward that the other expects (Clutton-Brock & Parker 1995), causing the costs of engaging in mutualistic behaviour to outweigh its benefits (Riehl & Frederickson 2016). Across sub-Saharan Africa, greater honeyguide birds guide humans to bees' nest, exchanging their knowledge of the locations of bees' nests for a food reward (beeswax) resulting from human honey-hunters' abilities to subdue bees with smoke, and open their nests using axes (Friedmann 1955; Isack & Reyer 1989). In this mutualism, one partner occasionally fails to do their part: humans may fail to harvest the nest or reward the bird, and a guiding honeyguide sometimes fails to show a human a bees' nest (Spottiswoode et al. 2016; Wood et al. 2014). The latter can occur when a honeyguide prematurely stops guiding before any destination is reached. However, according to centuries of African Indigenous accounts (Figure 4.1), failure to guide to bees can also occur when a honeyguide deliberately guides humans to an animal dangerous to humans such as a lion, buffalo, elephant, rhino, or large venomous snake, or occasionally a carcass (Friedmann 1955; Isack 1987).

The first account in scientific literature of honeyguides guiding humans to such non-bee species dates from 1776, when Khoe-Sān honey-hunters in the Western Cape of South Africa recounted being occasionally guided to "dangerous animals" (Sparrman 1777). Seventy-nine years later, David Livingstone attempted to evaluate the frequency of such behaviour by asking East African honey-hunters whether they had been guided by a honeyguide to anything but a bees' nest, and reported that "Only one out of the 114 could recall that he had had such an experience although all had been guided on a great many occasions" (Livingstone 1858). Later, in his landmark study of honeyguides in Kenya, Hussein Isack reported that "A common belief that the Boran share with several other communities in Africa is that the bird often guides man to animals such as lions, buffalos, elephants, rhinos, large poisonous snakes or to enemies or murderers from a hostile tribe… It is believed that the bird resorts to this abnormal behaviour as a result of man's failure to spare some food for it after the bird had helped him discover a [bee] colony” (Isack 1987).

Unfortunately, few published accounts of guiding to non-bee animals across Africa include first-hand observations, and the ability of honeyguides to deliberately guide to non-bee species has typically been treated with scepticism by both ornithologists (Friedmann 1955; Short and Horne 2001) and by some honey-hunters (Isack 1987). Such scepticism is understandable given the temptation by observers to attribute incidental encounters with such animals as deliberate on the part of the honeyguide. It is nonetheless striking that reports of this phenomenon are widespread across Africa (Figure 4.1) (Isack 1999).

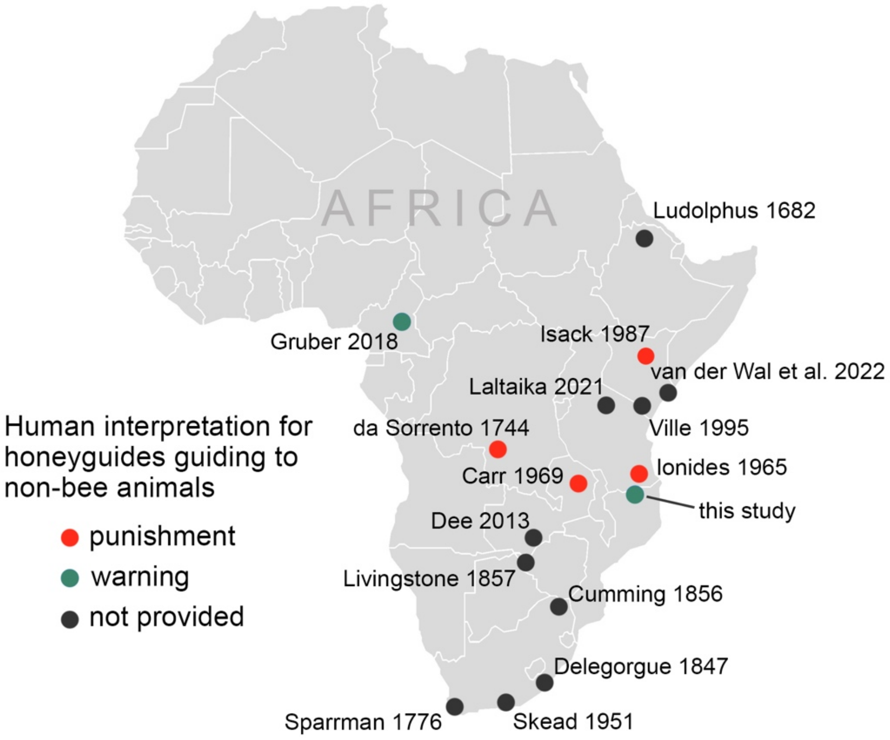


Figure 4.1. Published accounts from 14 African honey-hunting cultures of humans being guided by honeyguides to non-bee animals, with cultural explanations (where provided) for this behaviour.

If honeyguides deliberately guide to non-bee animals, it is not known why such behaviour would occur and whether it is adaptive. Human cultural interpretations for such a behaviour vary across Africa with the most influential explanation being that honeyguides do so to punish a person for prior failure to reward it with beeswax following a honey harvest (da Sorrento 1744; Friedmann 1955; Ionides 1965; Carr 1969; Isack 1987). This has, to our knowledge, only been documented from four honey-hunting cultures (Figure 4.1), but strongly appeals to the human imagination and is widely repeated. Evidence for punishment between heterospecifics, where one partner sacrifices payoffs from interaction to harm a cheating partner, has rarely been observed among nonhuman animals (Jensen 2010; Raihani & Bshary 2019; Raihani et al. 2012), yet is known from client-cleaner fish mutualisms (Bshary & Grutter 2005).

In contrast, some honey-hunting cultures (including the Yao culture which is the focus of the present study) believe that when honeyguides guide a human to animals other than bees, the honeyguide is acting altruistically by warning a human of a danger nearby (Gruber 2018). Meanwhile, other cultures do not provide a clear functional interpretation for this behaviour and accept that “bad honeyguides” rarely yet deliberately guide people to animals other than bees (Isack 1999). Some writers dismiss the idea that honeyguides guiding to dangerous animals or other objects is deliberate, and instead consider these encounters to be chance events en route to a bees’ nest (Friedmann 1955; Short & Horne 2001). Across a wide variety of accounts, what remains consistent is the reported infrequency of honeyguides guiding to non-bee animals, even in areas where honeyguide-human cooperation is common (e.g., Isack 1987; Livingstone 1857). Infrequent observations of an apparently rare behaviour would also have likely reduced further as human-honeyguide cooperation has diminished across the African continent (Isack 1999; van der Wal et al. 2022a).

In this study, we present recent quantitative data from interactions in Mozambique between Yao honey-hunters and honeyguide, which corroborate historical accounts that honeyguides deliberately guide humans to non-bee animals. We review five biological hypotheses (Table 4.1), some of which draw on human cultural explanations for why honeyguides may guide to non-bee animals, and generate testable predictions for each. Finally, prompted by our first-hand observations, we use additional field data to retrospectively evaluate certain predictions of each hypothesis.

Material and methods

Study site

This study was conducted in a 280 km^2 area within the Niassa Special Reserve in northern Mozambique (Lloyd-Jones et al. 2022; Spottiswoode et al. 2016). This area is inhabited and utilized by Yao honey-hunters who live in Mbamba village (12°12'S, 38°01'E), which has a population of ca. 2,000 inhabitants, including > 20 professional honey-hunters (Lloyd-Jones et al. 2022). In this miombo woodland area, honeyguide–human interactions occur daily, under conditions likely comparable to those under which the mutualism evolved (see Cram et al. 2023; Lloyd-Jones et al. 2022; Spottiswoode et al. 2016 for further details of the study system). Yao honey-hunters consistently reward honeyguides with beeswax of a varying amount following a harvest (Lloyd-Jones et al. 2022), although the act of harvesting a bees' nest can also enable a honeyguide to benefit from wax via access to the tree cavity containing leftover beeswax. Yao honey-hunters do not reward honeyguides when they are guided to a bees' nest that they do not harvest, since no wax is yielded. This rewarding behaviour of Yao honey hunters is directly linked to a belief that failure to do so results in honeyguides being less cooperative in the future, both by guiding to fewer bees' nests and by guiding to other dangerous animals instead.

Data collection

Given that guiding to non-bee animals appears to be rare, it was not possible to design a study specifically documenting it. Rather, we collected data opportunistically during other studies and experiments with honeyguides.

Four datasets are used here. First, four first-hand accounts of honeyguides guiding honey hunters to non-bee animals were recorded in 2018 from separate honey hunts under natural conditions and included visual, spatial, and in some cases, acoustic data. We used these data to describe our direct observations of honeyguides guiding to non-bee animals. Second, 108 records of honey hunts (defined as a single human-honeyguide interaction with a unique starting point) between January 28 and December 22, 2018. We used these data to calculate overall rates of guiding to bees' nests compared to non-bee animals. Third, we used a subset of 24 honey hunts (from the 108 honey hunts) for which we have complete GPS tracks of guiding interactions, and a further subset of 22 honey hunts with audio recordings of honeyguide vocalizations, recorded between May 18 and June 27, 2018. Twenty of these honey hunts ended with the honey hunter finding bees, and four ended with the honey hunter finding an animal other than bees. We used the 24 GPS tracks to analyse spatial movement patterns and used the 22 audio recordings to analyse honeyguide vocalizations while guiding. Some of these honey hunts were recorded on the same day (mean number of honey hunts per day ± SE = 1.71 ± 0.29, n = 24), but when this was the case, the starting points were < 1500 m apart, making it likely that different honeyguide individuals were involved. In the last dataset, we selected 28 honey hunts that occurred in close (< 1500 m) proximity to each other within a 7-day period. We used these interactions to calculate rates of honeyguide behaviour in relation to prior rewarding behaviour by humans (i.e., provision of beeswax) by humans.

Although we have conducted research at this site since 2013, we only analysed data from 2018, given that all our observations of being guided to non-bee animals were made in this year, and we wanted to ensure that environmental conditions were comparable for guiding events with different outcomes.

To initially locate the bees' nests, one researcher (Claire Spottiswoode or myself) accompanied two Yao honey hunters on a honey-hunt as they elicited guiding behaviour from greater honeyguides using culturally determined, locally specialized calls, given either naturally or using controlled speaker playbacks (repeated loops of either the locally specialized call or, as a control treatment, a human calling his name) as part of behavioural experiments following methods in Spottiswoode et al. (2016). Honey hunts involving such playbacks contributed one of the four instances of guiding to dangerous animals, and six of the 28 guiding events contributed to our post hoc analyses of whether nonrewarding behaviour by honey hunters is more likely to precede being guided to non-bee animals. In these seven instances, the playback was either a repeated loop of a human calling their name (n = 3), used as a control sound, or a specialized "brrr-hmm" sound (n = 4). All honey hunts began at intervals along vehicle tracks at least 500 m apart, and at least 1500 m apart when conducted on the same day, to reduce the confounding effect of prior interactions with honeyguides.

For spatial analyses of guiding behaviour to bees' nests or non-bee animals, I used GPS tracks of 24 guiding events (points recorded at set 1 s intervals using Garmin eTrex 30, Garmin USA), which all involved natural honey hunter calls to honeyguides, except one guiding event to a puffadder which was accompanied by control playbacks (described above). The final destinations of all guiding events (whether bees' nests or other animals) were previously unknown to us or the honey hunters.

For audio analyses of honeyguide calls, I used stereo audio tracks recorded on 22 of these events (two of which involved guiding to non-bee animals), using a unidirectional Sennheiser ME66 (Sennheiser Inc, Wennebostel, Germany) microphone recording to a Sony PCM-M10 (Sony Group Corporation, Tokyo, Japan), continuously aimed at the honeyguide. Acoustic recordings began prior to guiding and continued until the bees were located. All audio tracks were saved as Linear PCM (WAV) files at 96.00 kHz/24 bit and were reviewed, clipped to length, and normalized to -3.0 dB using Audacity version 3.0.5 (Audacity Team 2022). Raven Pro v. 1.6.1 (Center for Bioacoustics Cornell, 2019) was then used to display sounds as spectrograms, from which we manually selected bounding boxes for individual syllables from within 'chatter' and 'indication' call types (Isack 1987). Following Isack (1987), we distinguished between typical 'chatter' calls given by honeyguides while guiding, and 'indication' calls which are also sometimes given while guiding but characteristically given as the honeyguide approaches the bees' nest, prior to going silent (Appendix to Chapter 4).

Data analyses

We tested whether honeyguides were more likely to guide humans to non-bee animals after not being rewarded by humans (i.e., when a human follows a honeyguide to a bees' nest but does not harvest; Figure 4.4) by focusing on 11 honey-hunts that had been preceded by two or more prior honey hunts within 1500 m or less, within the previous 7 days. In total, there were 28 prior honey-hunts (two were counted twice, due to their proximity in different directions to two different harvests). For each of the 11 focal honey-hunts, we calculated the proportion of prior honey-hunts which resulted in a bees' nest harvest and consequently a wax reward versus finding a bees' nest but choosing not to harvest (Figure 4.4). We next compared the proportion of prior rewards for focal honey-hunts that involved being guided to non-bee animals (4 of the 11 focal honey-hunts), versus honey hunts that involved being guided to bees' nests (7 of the 11 focal honey-hunts). We ran a generalized linear model (GLM) with a binomial logit link function to test the effect of prior reward rates on the binary outcome of being guided to a bees' nest or to non-bee animals. We visualized residuals and plotted them against fitted values to assess model assumptions, which indicated no severe deviations from linearity on the logit scale, no strong outliers, and approximate homoscedasticity.

We selected the < 1500 m and 7-day limits for the above dataset under the assumption that repeated interactions with the same individual honeyguide were possible within such limits, although it is plausible that many honeyguides could have been involved in prior interactions, given high honeyguide densities at this site (Cram et al. 2023). This represents an imperfect best attempt at detecting a relationship between past rewarding behaviour and guiding to non-bees, with the parameter values supported by past work at this location showing that honeyguides can move over an area with a radius of at least 1500 m over short time periods (Spottiswoode et al. 2016).

Three measures of human movement were extracted from GPS tracks of honey hunters following honeyguides: distance guided, speed, and sinuosity. For distance guided, start points were determined from the simultaneous audio recordings as to where the honeyguide arrived and first “chattered” to the human, and stop points as to where the honeyguide reached either a bees' nest or a non-bee animal. Speed was measured from the GPS track of the honey hunter carrying a GPS. The sinuosity of human movement was the ratio of actual distance travelled to the distance of the shortest as-the-crow-flies path, measured using GPS tracks (Wood et al. 2021).

We used R v. 4.0.3 (R Core Team 2023) for all statistical analyses. To test whether the distance guided to non-bee animals was statistically different from that when guided to a bees' nest, we used a Mann–Whitney U test because as the data violated assumptions of normality and homogeneity of variances (tested using Shapiro–Wilk and Levene's tests). Similarly, to test whether average speed while being guided to a bees' nest differed from that while being guided to non-bee animals, we used a Wilcoxon rank-sum test because these data solely violated the assumption of normality (assessed using Shapiro–Wilk and Levene's test for homogeneity of variance). To test for differences in the sinuosity of tracks ending at non-bee animals compared to those ending at bees' nests, we used a nonparametric Mann–Whitney U test because preliminary Shapiro–Wilk and Kolmogorov–Smirnov tests indicated that these data violated the assumptions of normality and homogeneity of variance distributional assumptions.

To analyse acoustic differences between honeyguide “chatter” and “indication” calls, we used a principal components analysis (PCA) using the “stats” package in R (Bates et al. 2015), based on 20 acoustic variables for each of the “chatter” and “indication” syllables (details in Appendix to Chapter 4) extracted using the “warbleR” package (Araya-Salas and Smith-Vidaurre 2017).

Results

Honeyguides only rarely guide to animals other than bees

At our study site in northern Mozambique, the observed rate of being guided to animals other than bees in 2018 was 3.7% (4 of 108 guiding events leading to a distinct destination). It was 0% in my and Claire Spottiswoode's own personal experience of guiding events leading to a distinct destination (i.e, were 'successful') at this location during 2013–2017 and 2019–2024 (approximately N = 350), and one honey-hunting colleague (Musaji Muamedi) also experienced no other events during this period as an active honey-hunter (approximately N = 330 honey-hunting trips during 2017–2022).

Direct observations of honeyguides guiding to non-bee animals

We have been guided by a honeyguide to a non-bee animal on four occasions:

(1) On 18 May 2018, Claire Spottiswoode and one other honey-hunter (Issufo Mussa) were guided by an adult female honeyguide while conducting a playback experiment (details in Methods). Guiding began at 09:05 h (all times are local time: UTC+2) and continued until 09:26 h when the honeyguide went silent (as is typical behaviour signalling arrival at bees; Isack & Reyer 1989) near an adult puffadder (*Bitis arietens*) in short grass. We had followed the honeyguide for 838 m walking distance (Figure 4.2), during which the honeyguide vocalized with 'chatter' calls and at the destination flew with low swooping flight in the same way as when guiding to bees. This interaction was not audio recorded.

(2) On 13 June 2018 one honey-hunter (Orlando Yassene) and I, during a completely natural honey-hunt (i.e., one in which all interaction decisions and vocalizations were being made by Yao honey-hunters, were guided by an adult male honeyguide to a bees' nest. On arrival at the tree with bees, the honeyguide went silent. After 65 s the honeyguide began calling again and guided our human party onward, at 08:40:10 h, to what we presumed were other bees, given that honeyguides commonly lead humans to multiple bees' nests in succession (Friedmann 1955; Isack 1987; Spottiswoode et al. 2016). The honeyguide flew ahead of the honey-hunter party, chattering continuously, stopped and then doubled back ca. 10 m, perching in a tree adjacent to a dead greater galago (*Otolemur garnettii*) splayed out in short grass, at 08:44:00 h. Audio recordings of this honeyguide were very faint due to background noise and so not used in acoustic analyses. The galago appeared intact and was unlikely to have been there for more than

24 hours, showing no sign of decomposition or being scavenged. The honeyguide remained silently perched in adjacent trees for the full duration we were there (ca. 10 min).

(3) On 18 June 2018, whilst recording honey-hunting audio signals during another natural honey-hunt, myself and two Yao honey-hunters (Rui Francisco, Aloisi Chole Sindi) were guided by an adult female honeyguide (starting 10:53:59 h) directly to an adult black mamba (*Dendroaspis polylepis*) at 11:00:16 h. The snake was coiled up and basking on a termite mound. Throughout, the honeyguide showed all the characteristic behaviours of guiding to bees: a loud chattering call initially, strong continuity of chattering to humans, who were responding using traditional “brrr-hmm” signals, staying within sight 15–25 meters ahead of the party, and a change from a ‘chatter’ call to the ‘indication call’ (a signal observed by us, and widely reported by honey-hunters, to be given when nearing a bees’ nest; Isack 1987) 1 m 15 s before arriving at the snake. The honeyguide flew low over the snake and perched above it, in the same way as near a bees’ nest, and went immediately silent. When we approached within ca. 10 m, the snake disappeared into the termite mound. We systematically searched (radius 20 m) for bees’ nests for ca. 10 min, but we found none. Throughout this search the honeyguide remained silently perched nearby, first in the tree above the snake and then in adjacent trees.

4) On 22 June 2018, whilst recording honey-hunting audio signals during a natural honey-hunt, myself and two Yao honey-hunters (Carvalho Issa and Armando Pita) were guided by an adult male honeyguide to a southern African rock python (*Python natalensis*) basking at the base of a tree. Within 10 s of arriving within 5 m of the snake, it went into a cavity at the base of the tree. The honeyguide had guided us 5 minutes earlier to a bees’ nest (which the honey-hunters decided not to harvest), then resumed chattering and flew onwards at 10:46:22 h. The party followed the honeyguide for 75 meters and arrived at the python at 10:48:34 h. The honeyguide made ‘indication’ calls as it flew into the tree above the python, and then perched silently 6–7 meters above the hole in the tree the python went into. On this occasion, as with the three preceding records, the Yao honey-hunters reported at the time that they were certain that they had been guided to this location deliberately by the honeyguide.

On other occasions, we have encountered numerous snakes, and occasionally elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), and lion (*Panthera leo*) while being guided by honeyguides, but we consider these to be incidental encounters since in most cases it was clear from the honeyguide's behaviour that it was leading us beyond these animals. On one occasion our interpretation differed from that of the honey hunters we accompanied: on June 11, 2023 we encountered a Mozambique spitting cobra (*Naja mossambica*) while being guided, and the honey-hunters we accompanied reported post hoc that the honeyguide had deliberately guided us to the snake. However, the honeyguide did not pause or cease calling at the location where the snake was sighted, and continued to guide us to a bees' nest, so we consider this a false positive (details in Appendix to Chapter 4).

Honeyguide spatial behaviour when guiding to non-bee animals is similar to when guiding to bees

Based on the subset of tracks with high-resolution GPS data, the distance over which honeyguides guided us to non-bee animals (range: 75–838 m, mean ± SE = 329 ± 173 m, *n* = 4) was not significantly different (Mann–Whitney U test; W = 36, p = 0.79, *n* = 24) from the distance over which honeyguides guided us to bees (range: 73–890 m, mean ± SE = 308 ± 47 m, *n* = 20). Walking speed when being guided to non-bee animals (range: 2.08–2.50 kph, mean ± SE = 2.3 ± 0.09 kph, *n* = 4, Figure 4.2) was also not significantly different (Wilcoxon rank sum test; *n* = 4, 20, W = 35.5, p = 0.76) from walking speed when being guided to bees (range: 1.08–3.49 kph, mean ± SE = 2.5 ± 0.15 kph, *n* = 20). Lastly, the sinuosity of the GPS tracks recorded en route to non-bee animals (range: 1.09–1.66, mean ± SE = 1.30 ± 0.13, *n* = 4) was not statistically different (Mann–Whitney U test; n = 24, W = 46, p = 0.68) from track sinuosity when guided to bees (range: 0.92–6.57, mean ± SE = 1.71 ± 0.30, *n* = 20).

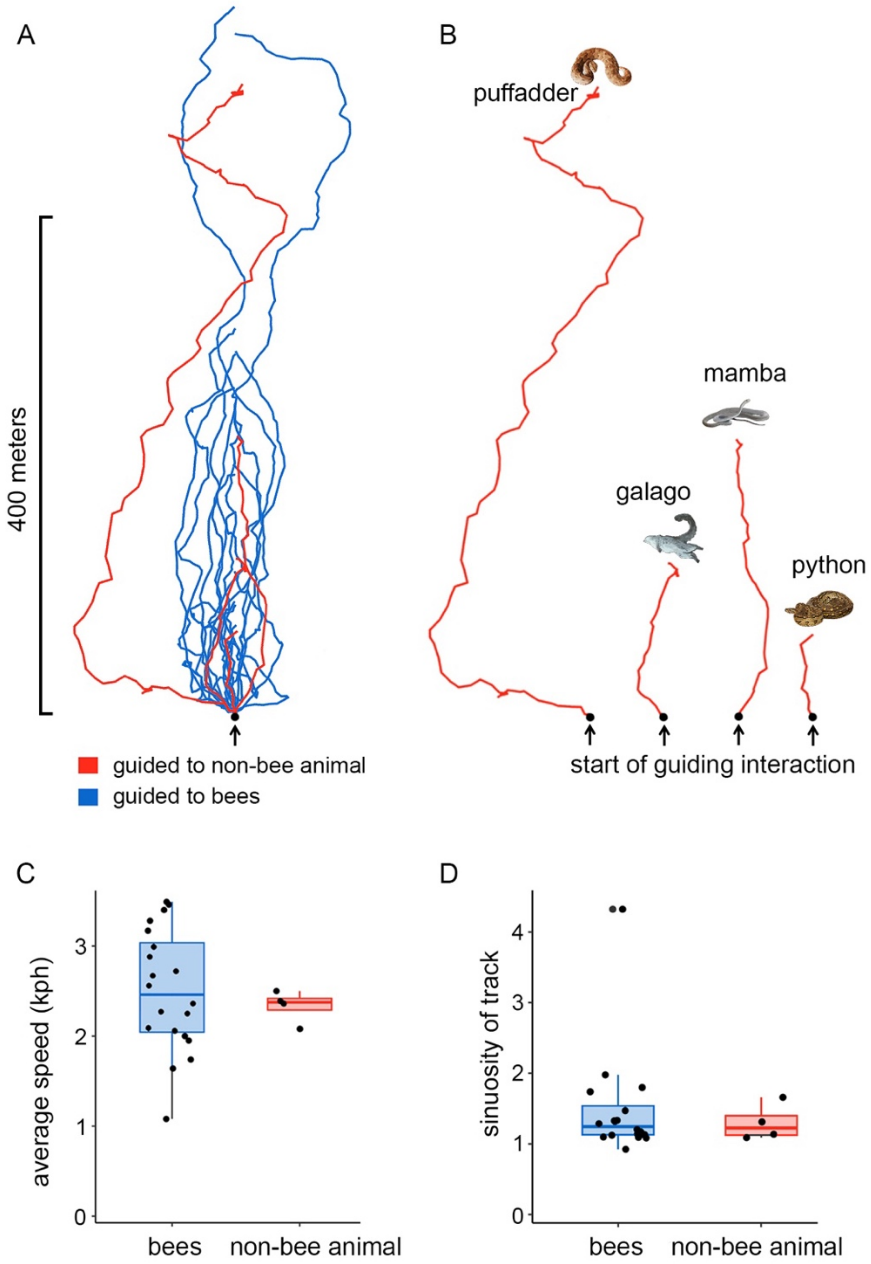


Figure 4.2. (A) GPS tracks of 20 guided honey hunts ending at bees' nests versus four guided honey hunts to non-bee animals (all tracks rotated to align along a straight vertical line between their start and end points). (B) GPS tracks of four guided honey hunts to non-bee animals plotted to scale but all oriented vertically. (C) Average speed (kph) of guided honey hunts to bees' nests and non-bee animals. (D) Sinuosity (the ratio between GPS distance and straight-line distance) for honey hunts to bees' nests compared to honey hunts ending at non-bee animals.

Honeyguides emit the same call when nearing non-bee animals as when nearing bees

To test whether honeyguides produce similar calls when guiding honey hunters to bees as to non-bees, we used audio recordings from two instances of guiding to non-bees and from 20 instances of guiding to bees' nests. On both of the former, the honeyguide altered its calls from the "chatter" call (given initially upon guiding and over much of a honey-hunt) to "indication" calls (Figure 4.3). This switch in call type was observed in 17 of 20 (85%) audio-recorded events of guiding to bees' nests (Figure 4.3A). The mean straight-line distance (from the destination) at which the "indication" calls started to be produced when being guided to bees was mean ± SE = 63 ± 15.4 m, *n* = 16, and when being guided to snakes was mean ± SE = 16 ± 1 m, *n* = 2). On all four occasions of being guided to non-bees, the honeyguide went silent upon arrival at that location, and in three of four instances perched within sight in an adjacent tree in the same way as when guiding to bees (pers. obs., also Isack 1987; Short 1988; Short and Horne 2001).

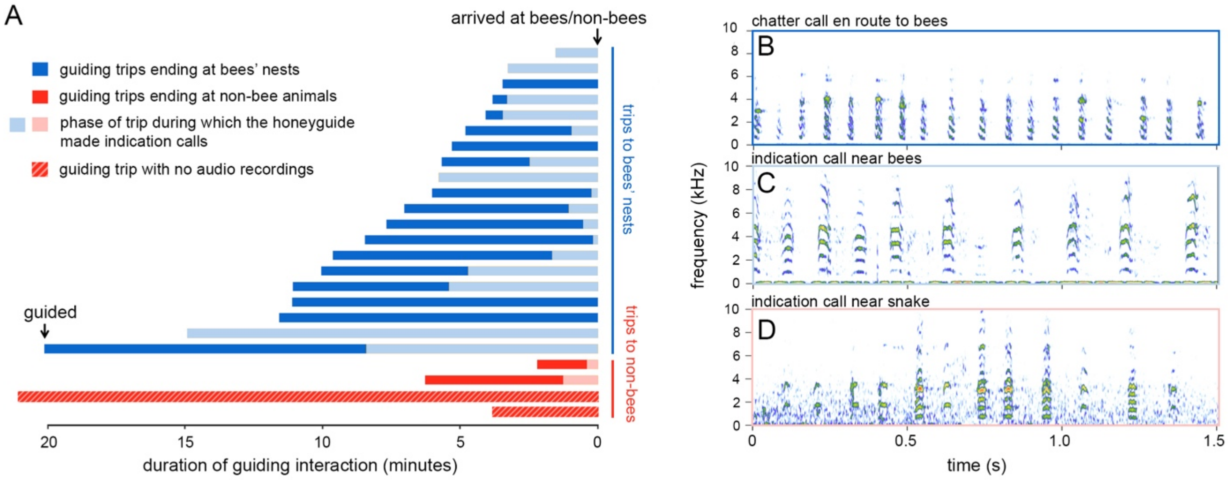


Figure 4.3. (A) Graphical representation of the overall duration and call-types given by honeyguide over 24 GPS-recorded honey-hunts, of which 22 were audio recorded. Change in tone from dark blue or red to light blue or red indicates the transition in 'chatter' guiding calls to 'indication' guiding calls, which are typically used in closer proximity to bees (Isack 1987). Spectrogram of: (B) typical chatter call given by a honeyguide en route to a bees' nest, (C) 'indication' calls when guiding to bees, and (D) 'indication' calls when guiding to a black mamba snake.

Guiding to non-bee animals is no more likely after non-harvests by humans

For an imperfect test of whether honeyguides were more likely to guide humans to non-bee animals following non-rewarding behaviour by humans, we compared the proportion of honey-hunts in the same area which were rewarded prior to being guided to non-bee animals, versus prior to being guided to bees' nests (Figure 4.4). Honeyguides guided us to animals other than bees following prior reward rates of 0.5, 0, 0.75, and 0 (Figure 4.4), and to bees' nests following prior rewarding rates of 0.5, 1, 0.5, 0, 0, 1, 1 (Figure 4.4). While recognizing that the dataset is small, we found no significant effect of prior rewarding rates on the likelihood of being guided to nonbee animals compared to bees (Generalized Linear Model, Estimate = −1.69, SE = 1.71, z = −0.99, p = 0.32).

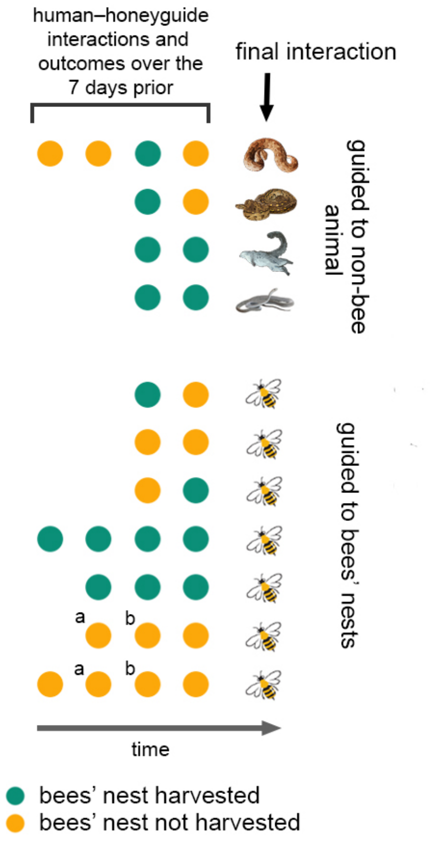


Figure 4.4. (A) Bees' nests found with the cooperation of a honeyguide, and whether or not they were harvested (leading to a reward for honeyguides), in 11 small subsets of our study area, with labels indicating whether we were subsequently guided either to non-bee animals (n = 4; animals illustrated are, from the top, puffadder, southern African rock python, greater galago, black mamba), or to bees (all *Apis mellifera*; n = 7). (B) Summary of guiding outcomes (i.e., being guided to bees or non-bee animals) in relation to prior patterns of reward.

Literature review and five hypotheses for guiding to non-bee animals

We found 20 published references to honeyguides guiding humans to non-bee animals, originating from nine countries (original quotations and sources are given in Appendix to Chapter 4, and geographical locations, dates, and interpretations are summarized in Figure 4.1). Of these 20 published references, five directly state the local human cultural interpretation for why honeyguides guide to non-bee animals (four are punishment, one is an altruistic warning). We do not consider in depth here the hypothesis that honeyguides may benefit from guiding humans to dead animals or carcasses, either because they benefit from the insects on the carcass (Delegorgue 1847) or because the flies at a carcass are a bee-like stimulus (Friedmann 1955). This is because we have neither observed nor found any reports of honeyguides feeding on carcasses or flies at carcasses. In Table 4.1 we present five hypotheses explaining this behaviour, together with their testable predictions. Hypotheses (1) to (3) have been previously proposed (da Sorrento 1744; Friedmann 1955; Isack 1987; Sparrman 1777) whereas (4) and (5) are proposed here for the first time. Briefly, these hypotheses are that guiding to animals other than bees is (1) the result of an *incidental encounter* occurring en route to a bees' nest, which humans mistakenly perceive to be the destination; (2) *punishment* of nonrewarding humans; (3) an *altruistic warning* to rewarding humans; (4) *recruitment* of mobbing partners; and (5) a *cognitive recall error* relating to how honeyguides store spatial information about memorable objects in the same way as they do bees' nests.

Discussion

In this study, we present first-hand data supporting centuries of assertions by a range of African honey-hunting cultures (Figure 4.1) that honeyguides rarely but intentionally guide honey-hunters to animals other than bees. Honeyguides guided us to three snake species and a dead mammal, in each case stopping at the animal and producing “indication” calls, in the same way as when a honeyguide has arrived in the vicinity of a bees’ nest. Furthermore, on three of the four observations of guiding to non-bee animals, honeyguides flew low over the snakes, which is a cue of arrival at bees’ nests located low down (Isack 1987 and pers. obs.). The track sinuosity, distance followed, and timing of when honeyguides produced “indication” calls prior to arriving at non-bee animals were all within natural ranges observed when guided to bees (Figure 4.4). While the small sample size means we have to interpret these findings with caution, taken together, they are inconsistent with the first hypothesis, that encounters with these animals are incidental occurrences en route to bees (hypothesis i, Table 4.1).

Next, we cautiously evaluate our field data against three functional hypotheses for why honeyguides deliberately guide humans to animals other than bees: as punishment, as an altruistic warning, or to recruit mobbing partners.

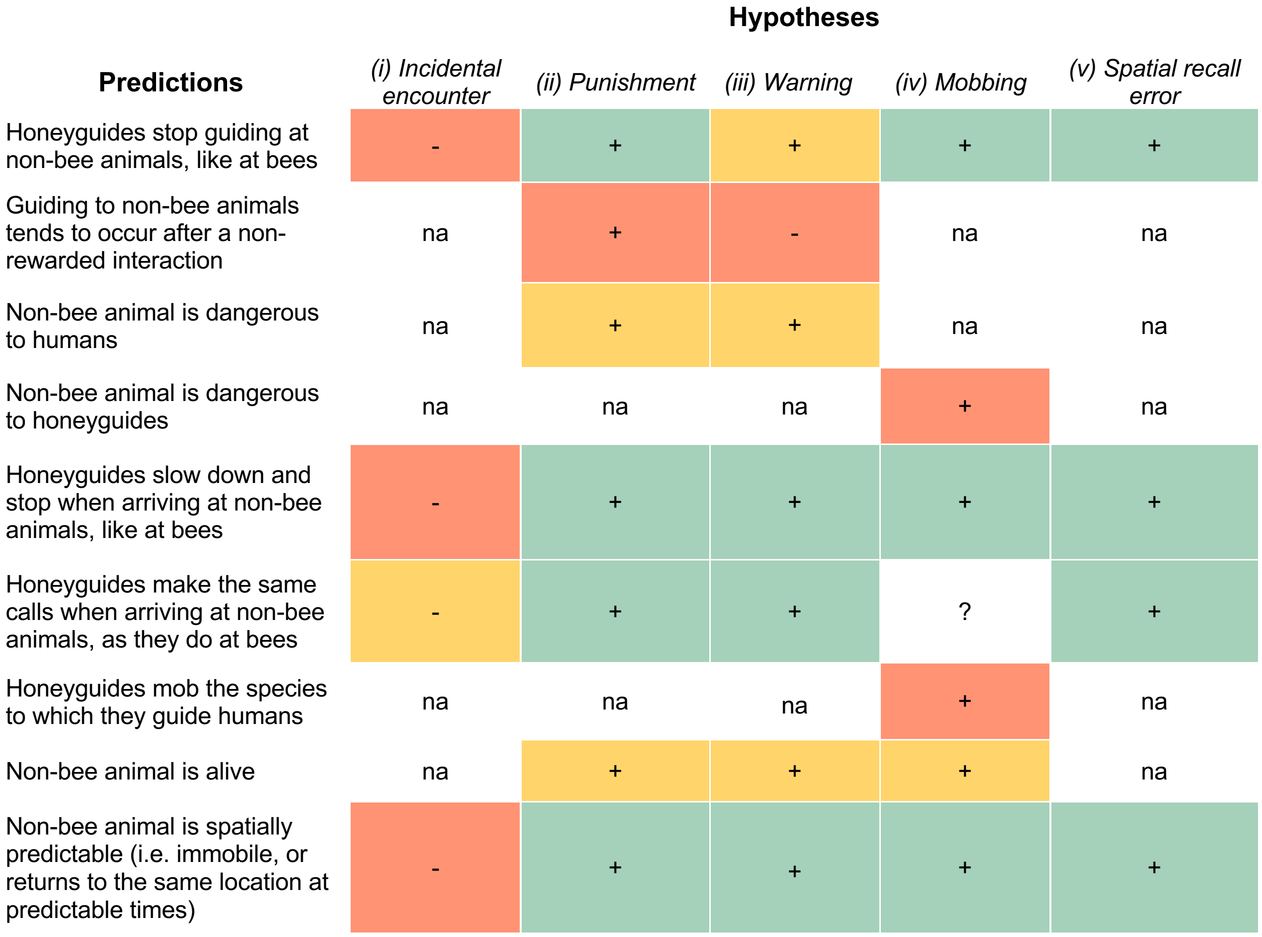
First, if punishment towards humans for non-rewarding behaviour is adaptive for honeyguides, then being guided to non-bee animals rather than bees should follow non-rewarding behaviour by humans, and encounters with these non-bee animals should have the potential to negatively impact the human(s). Neither of these predictions was supported: the degree to which honeyguides (not necessarily the same individual) in the vicinity had previously received a beeswax reward for cooperative behaviour did not predict whether we were subsequently guided to bees or non-bees, albeit in a small sample (Figure 4.4). In one instance, a honeyguide guided us to bees after taking us to a python, and we were guided to a dead galago immediately after being guided to and harvesting a bees' nest. Finally, the non-bee animals were largely non-threatening to humans, since Yao honey-hunters regularly encounter snakes, and even the black mamba, an agile and feared species, attempts to evade humans as a first response (Spawls et al. 2018), which is considered by Yao honey hunters to be far less threatening than an unexpected encounter with a large mammal such as buffalo, elephant, and hippopotamus.Further to this empirical evidence, there are theoretical objections to the evolution of punishment by honeyguides. Punishment would require individual birds to: (a) recognize cheating individual honey-hunters, (b) have repeat encounters with these cheating individuals, and (c) cause humans to alter their behaviour to be more cooperative in future encounters (Raihani et al. 2012). These conditions are unlikely to be met, given that honey-hunters interact with many different honeyguides within the large area (> 812 km^2) over which honey-hunters range, likely resulting in a low re-encounter rate (Cram et al. 2023). Moreover, certain other honey-hunting cultures elsewhere in Africa intentionally withhold wax rewards from honeyguides, by either pretending not to spot bees' nests or choosing not to harvest so that the honeyguides "stays hungry" and shows them more bees' nests; yet there is no evidence that honeyguides are less likely to cooperate with, or are more likely to "punish" humans in these populations (e.g. Isack 1987; Laltaika 2021; van der Wal et al. 2022b; Wood et al. 2014).

Even in cultures that deliberately reward honeyguides from harvested bees' nests (such as the Yao culture in this study), honeyguides often experience unintentional non-rewarding behaviour. For example, in the miombo woodland habitat of our study area, a tree containing a bees' nest can be either too big to harvest or too hard to cut into with an axe, or the bees' nest may appear to not contain enough honey to merit the effort. The cost to humans of depriving honeyguide partners appears to be low, since honeyguides continue to cooperate regularly across varied cultural settings (Laltaika 2021; van der Wal et al. 2022a; Wood et al. 2014). Furthermore, unlike in other systems of punishment (Raihani et al. 2012), in the honeyguide-human system there is no scope for coercion: neither humans nor honeyguides can force their cooperative partners to cooperate. We conclude that there is neither empirical nor theoretical support for a punishment hypothesis of guiding to non-bees.

Second, in contrast to a punishment hypothesis, some cultures interpret being guided to dangerous animals as a form of *altruistic warning* to the humans of danger ahead (hypothesis iii, Table 4.1). These cultures include the Yao honey-hunters with whom we collaborate in this study, the wider Yao honey-hunting community (pers comms.), and at least some other cultures (Gruber 2018). This hypothesis makes certain similar predictions to those for punishment (i.e., that honeyguides should guide deliberately to living but spatially predictable animals dangerous to humans). However, unlike the punishment hypothesis, a warning hypothesis predicts that guiding to non-bees should occur following consistent wax rewards. This was not supported, since we did not detect higher rates of guiding to non-bee animals in areas where honeyguides had been previously rewarded, albeit in a limited sample given the rarity of guiding to non-bee animals (Figure 4.4).

Third, we propose as an alternative hypothesis that honeyguides may guide humans to recruit them as mobbing partners towards non-bee animals which they may perceive as a threat (e.g., snakes, predatory birds), much as other birds recruit other species as mobbing partners (Dutour et al. 2017). The natural history of these species does not clearly support this idea, since two of the snake species guided to (python and puffadder) are terrestrial and relatively slow-moving, and small, agile, arboreal birds such as honeyguides are likely not an important part of their diet (Short 1988). In general, species in the honeyguide family (Indicatoridae) are typically cryptic and rarely mob other species (Hockey et al. 2005), and greater honeyguides only make themselves conspicuous when singing or when chattering to elicit cooperation from humans (Fry et al. 1988). Thus, a mobbing function seems unlikely.

Table 4.1. Five hypotheses, with associated predictions, for why honeyguides guide humans to the location of non-bee animals: (i) a null hypothesis that these are *incidental encounters* en route to a bees' nest, or that it is deliberate and (ii) functions as *punishment* of non-reciprocating humans, (iii) functions as a cooperative *warning* signal to humans, (iv) functions to recruit *mobbing* partners, or (v) results from a cognitive *spatial recall error* regarding the destination of the guiding event. Positive and negative symbols indicate whether or not each hypothesis makes this prediction, and 'na' indicates that a prediction is not relevant to the hypothesis. Green cells indicate empirical support for the designated prediction, orange cells indicate no support, and yellow cells indicate mixed support.



	Hypotheses				
Predictions	*(i) Incidental encounter*	*(ii) Punishment*	*(iii) Warning*	*(iv) Mobbing*	*(v) Spatial recall error*
Honeyguides stop guiding at non-bee animals, like at bees	-	+	+	+	+
Guiding to non-bee animals tends to occur after a non-rewarded interaction	na	+	-	na	na
Non-bee animal is dangerous to humans	na	+	+	na	na
Non-bee animal is dangerous to honeyguides	na	na	na	+	na
Honeyguides slow down and stop when arriving at non-bee animals, like at bees	-	+	+	+	+
Honeyguides make the same calls when arriving at non-bee animals, as they do at bees	-	+	+	?	+
Honeyguides mob the species to which they guide humans	na	na	na	+	na
Non-bee animal is alive	na	+	+	+	na
Non-bee animal is spatially predictable (i.e. immobile, or returns to the same location at predictable times)	-	+	+	+	+

Instead, our data were most consistent with a fifth hypothesis (hypothesis v, Table 4.1): that honeyguides sometimes deliberately guide humans to a location where the honeyguide has previously encountered an animal, and which it has stored in its spatial memory, but then makes a *cognitive spatial recall error* about which locations correspond to a food reward. In this concept, the only difference between the honeyguide's behaviour when guiding to bees or non-bees is the erroneous selection of the destination. Spatial recall errors have been widely measured in scatter-hoarding bird species (Pravosudov & Roth 2013; Sonnenberg et al. 2019), and variation in spatial cognition can be influenced by environmental complexity (Branch et al. 2022; Roth et al. 2012), sleep (Rattenborg et al. 2011), and hippocampal neurogenesis (Leuner et al. 2006). It is also plausible that honeyguides may have genetic variation in their spatial cognitive ability, such as that recently demonstrated in scatter-hoarding, free-living mountain chickadees (*Poecile gambeli*). Such genetically linked variance makes spatial cognitive ability available for natural selection (Branch et al. 2022; Welkin et al. 2024).

A genetic basis for variation in spatial cognitive ability in honeyguides could provide an explanation for why honeyguide spatial error rates appear to be low since there should be strong selection for reliable spatial cognition in honeyguides given the key role of spatial information in honeyguide ecology. Although we currently lack a detailed understanding of honeyguide cognition, we know that honeyguides are ecologically heavily reliant on spatial memory. Both sexes cache food (pieces of high-quality beeswax: Isack 1987; Chapter 3) and can directly guide cooperating humans to bees' nests up to 1,500 m away (Isack & Reyer 1989), and as brood parasites females must locate and relocate numerous nests of their hosts (Spottiswoode & Koorevaar 2012).

The honeyguide foraging system for beeswax also has intriguing parallels to systems of caching and food retrieval found in other groups of birds. Corvid species annually find, hide, and retrieve up to 100 000 food items, termed "scatter hoarding" (Clayton et al. 2007; Vander Wall 1990). For example, Western scrub-jays (*Aphelocoma californica*) cache multiple food types year-round, and not only remember the location of food items, but also the food type and timing of caching (Correia et al. 2007). In comparison, honeyguides must first locate spatially scattered food sources (bees' nests), store the location of these possible future food sources, then recall them accurately when the opportunity to guide a honey-hunter arises, potentially from a novel direction (Isack & Reyer 1989). Unlike other scatter-hoarding bird species, which may have more time with which to recall spatial information, honeyguide encounters with humans are largely unpredictable to the bird in both time and space (Isack & Reyer 1989). This means that honeyguides need to make rapid decisions about where to guide a honey-hunter based on their current location, making occasional errors a possibility.

Collectively, our field data and historical accounts suggest that honeyguides guide humans to non-bee animals at a low rate which is tolerated by both partners, yet enough to culturally influences Yao honey-hunters. In informal discussions with 21 Yao honey-hunters, when asked "Why do you reward honeyguides after a honey-harvest?", all 21 honey-hunters consistently reported that they do so to motivate the honeyguide to (a) continue guiding to bees in the future, and also (b) altruistically guide them to nearby dangerous animals as a "warning." A low error rate by honeyguides is tolerated since the cost of guiding to a non-bee animal is similar to that of being guiding to a bees' nest that the human cannot harvest (i.e., no honey benefits for the human, no beeswax benefits for the bird). Such human cultural interpretations of even rare experiences could disproportionately influence human responses to this behaviour. For example, whether people consistently reward honeyguides or not can be wholly based on a belief in punishment should they fail to do so. Rapid cultural transmission can propagate human knowledge of even rare honeyguide errors, which in turn promotes future cooperation regardless of whether the human perception of that behaviour is positive (warning) or negative (punishment).

Conclusion

This study reviews and corroborates centuries of Indigenous African cultural knowledge asserting that honeyguides rarely but intentionally guide humans to non-bee animals (albeit with a small sample). Punishment is an appealing and widely repeated explanation, but our evidence suggests that this behaviour is unlikely to have evolved for this function, or as a form of altruistic warning to humans, or to recruit mobbing partners. Instead, the available evidence from our limited data best supports the hypothesis that guiding to non-bees arises from cognitive spatial recall errors that carry a low cost to individual honeyguides. Nonetheless, in some honey-hunting cultures, interpretations of this behaviour as punishment or warning may reinforce cultural traditions of rewarding honeyguides with beeswax. Such cultural interpretations may benefit honeyguides at the population level by providing increased overall beeswax rewards (Chapter 3). Such potential modest benefits may, along with low costs, reduce selection against cognitive errors.

CHAPTER 5

The impact of the human–honeyguide mutualism on miombo savannah woodlands

Abstract

Across sub-Saharan Africa, humans currently and historically have cut down trees to harvest honey from bee colonies (of *Apis, Melipona* and *Hypotrigona* spp.). Greater honeyguide birds (*Indicator indicator*), which lead humans to wild bees' nests, can alter the rate and size of bee colonies found by honey-hunters, and therefore the trees available to humans for cutting. I investigated tree cutting due to honey-hunting activity in Niassa Special Reserve, northern Mozambique, within a 627 km^2 area over six years (2017–2022) and quantified the species and size of trees found with bees. I found that bees occupied 63 tree species, but that the impact of tree cutting due to honey-hunting varied greatly among tree species. Honey-hunters' decisions about whether to cut down a tree with a bees' nest varied by tree size and species, likely influenced by their wood density, and the strength of traditional axes used to fell trees. Honeyguides influenced tree cutting by guiding honey-hunters to trees with smaller stems (of those cut down), and with bees' nests located higher up, than those found without the cooperation of honeyguides. Tree cutting for honey around Mbamba village appears sustainable because the overall impact across the landscape was minimal (0.6/stems/km^2/yr); honey-hunters did not selectively target

low-density species; most trees cut down were of an intermediate size; and the number and species of trees cut down for honey did not change during 2017–2022 for all but two tree species. Additionally, in demographic models projecting population trends for the four most frequently cut species, tree cutting did not lead to a decline of trees big enough to host bees. Overall, at the landscape level the influence of honey-hunters on tree populations was low, with human-honeyguide cooperation likely further reducing this impact.

Introduction

Miombo savannah woodlands are the most widespread woody habitat type across southern Africa (Frost 1996; Syampungani et al. 2009) and support the livelihoods of around 100 million people (Dewees et al. 2010). These warm, dry woodlands are characterized by the dominant tree genera *Julbernardia, Brachystegia* and *Isoberlinia*, and cover around 1.9 million km^2 (Dziba et al. 2020) across Angola, Zambia, southeastern Democratic Republic of Congo (DRC), western and southern Tanzania, Zimbabwe, central and northern Mozambique, and northern Malawi (White, 1983; Campbell 1996). Miombo woodlands host c. 8,500 plant species (White, 1983) and the trees, together with the diverse herbaceous understory, provide abundant nectar flow for honeybees (predominantly the subspecies *Apis mellifera scutellata*). Where relatively intact, miombo woodlands also support high densities of healthy honeybee colonies in natural nest sites in trees (Husselman 1998; Visick and Ratnieks 2023). In many parts of the miombo region, these are frequently harvested by human honey-hunters (Spottiswoode et al. 2016; Laltaika 2021), often with the assistance of greater honeyguide (*Indicator indicator*) birds that guide humans to bees' nests. In this chapter, I ask how honey harvesting and tree cutting by humans, with and without the assistance of honeyguides, affects miombo tree populations in habitat which supports bees, honeyguides, and people.

Humans have inhabited and shaped miombo savannah for at least 200,000 years (Morris 1970), and in many places rely on this habitat for timber and non-timber forest products, as they have historically (Coppinger et al. 2019; Ribeiro et al. 2019). In Niassa Special Reserve (hereafter 'Niassa'), northern Mozambique, a considerable proportion of the human population of c. 67,000 people (National Institute for Statistics 2017) still depends on harvesting wild honey to sustain their livelihoods, along with shifting agriculture and fishing (Spottiswoode et al. 2016; Cunliffe et al. 2009; Lubega et al. 2021; van der Wal et al. in review). The harvest of *Apis* honeybee nests occurs alongside the harvest of *Melipona* and *Hypotrigona* stingless bees (Spottiswoode et al.

2016), traditionally involving cutting out the honey using an axe (Figure 5.1). When the opening to a bees' nest is low (< 2 m above ground), honey-hunters in Niassa often cut a hole in the stem and leave the tree standing, but if the opening is high (> 2 m above ground), they typically cut down (fell) the entire stem. The latter results in the topkill (removal of the above-ground biomass) of the stem containing a bees' nest (see Box 1 for definitions). A fire is usually ignited near the base of the tree, to create smoke to calm the bees, and this can also damage the tree stems. However, since trees in miombo woodlands are often multi-stemmed, and since some species resprout prolifically when damaged and can also be clonal, the toppling of a tree stem for a honey harvest does necessarily spell death for the harvested tree.

Box 1: Terms and definitions used in this chapter	
bee tree	Any tree with a cavity containing an established colony of bees.
cut down (felled)	The action by a human of cutting down the above-ground portion of a tree.
fire trap	This is a cycle of repeated topkill due to fire, which can trap small trees in a cycle of above-ground biomass loss following resprouting. Fire trap dynamics can result in demographic bottlenecks which limit the transition of gullivers to canopy trees (Bond and van Wilgen 1996; Bond 2008).
gulliver	Small plants whose low stature and thin bark make then susceptible to top-kill by fire (Bond and van Wilgen 1996).
harvest	The process of cutting into (usually with an axe) a tree containing a bees' nest for the purpose of gaining access to honeycomb. Harvested trees may be felled or, if the entrance to the cavity is low (< 2 m above ground), harvested without felling the tree. The stems of harvested trees can be alive or dead.
recruits	Young trees (> 5 cm diameter) that have established from seeds or clonal suckers.
sapling	Small stems of up to 5 cm in diameter, and usually < 1.5 m tall (Bond 2017).
seedling	A newly germinated plant in its first year of growth.
topkill	The death or removal of the above-ground biomass of a tree from the base of the stem upwards. Topkill can occur due to natural causes such as fire and animal damage, or from human actions such as cutting or burning (Mtsetfwa et al. in review).
mortality	The death of a sapling or adult tree such that cannot reproduce. In savannah tree demography, adult background mortality rates range from 0.01 to 0.05 per annum (Higgins et al. 2000) and are important because they affect the longevity of woodland patches (Bond 2017).

The level of human influence on savannah tree communities is probably altered by the occurrence of greater honeyguide birds (hereafter 'honeyguides') which are abundant in our study location and guide humans to wild bees' nests (Spottiswoode et al. 2016; Cram et al. 2023; Chapter 2). Honeyguides and humans are partners in a reciprocal foraging mutualism in which a honeyguide leads human honey-hunters to wild bees' nests using vocal signals supplemented by visual cues (Isack 1989; Wood et al. 2014; Spottiswoode et al. 2016). The birds benefit from eating the beeswax left behind, after the humans have harvested the honey using an axe to access the nest and smoke to subdue the bees (Isack 1989, Diamond 1988, Lloyd-Jones et al. 2022). The humans benefit from information about where hidden bees' nests are located (Chapter 2).

Human-honeyguide mutualism is thought to have been once widespread across large swathes of sub-Saharan Africa, but now only remains fully functional in a small subset of the bird's range (Isack, 1989; Spottiswoode et al. 2016; Laltaika, 2021; Kilawi 2023; van der Wal et al. 2022). The mutualism tends to persist in places where: 1) suitable woodland and savannah habitat for bees remains, 2) knowledge of how to cooperate is maintained (van der Wal et al. 2022), and 3) wild honey remains a valued commodity and not yet replaced by commercially available sources of honey or sugar (Isack 1999). In Niassa, where honey-hunting continues to be practiced using only axes in a way which mirrors historical practices, a novel data collection technique (Chapter 2) provides a unique opportunity to quantify the impact and sustainability of tree-harvesting in a miombo savannah woodland. This also allows us to quantify the impact of honey-harvests of trees found due to honeyguide-human mutualism, compared to trees found without the cooperation of honeyguides (Chapter 2).

Tree-cutting for the purposes of honey harvesting is usually viewed as destructive and unsustainable by researchers, but not necessarily by local communities (Ntenga and Mugongo 1991; Fischer 1993; Syampungani et al. 2009; Coppinger et al. 2019; Ribero et al. 2019). A previous study in Niassa by Riberio et al. (2019) concluded that although harvesting rates appeared sustainable for *Julbernardia globiflora* and two other common tree species, for nine other tree species, honey harvesting practices had possibly, though inconclusively, reduced tree populations around Lisongole village in Niassa.

In this chapter I use three approaches to investigate the consequences of honey-hunting on the ecosystem. Each approach contributes to understanding a different aspect of how honey-harvesting and human–honeyguide interactions affect miombo savannah woodland, and whether the consequences of tree cutting are sustainable. A conservative definition of a demographically stable population is a population in which the size class distribution of individuals does not change over time (López-Hoffman 2006). Therefore, for honey-hunting to be sustainable, the rate at which the stems recruit back into the same size class needs to be equal to the rate at which they are being lost from that size class. This is affected by the number of seedlings and saplings in the population, the resprouting potential of the cut down tree, and the growth rates and background mortality rates of trees, among other factors (Twine and Holdo 2016). Because competition is a very strong constraint of tree growth rates in forests and woodlands (Bond 2017), topkill can potentially result in more rapid recruitment into the topkilled size class than would otherwise have occurred, which would promote sustainable use of the resource (Gotore et al. in review). All these factors need to be considered to understand the sustainability of honey-hunting activities in Niassa.

In the first section of this chapter, I describe spatial patterns of tree cutting due to honey-hunting activities around Mbamba village (Figure 5.2). I then describe the species and size classes of tree in which bees' nests were found ('bee tree preferences') and those which were cut down for honey ('honey-hunter preferences'). I then test how these honey-hunter preferences vary with tree sizes and species, and how these relate to the relative abundance of these species, leading to a range of impacts amongst species. From direct observations, honey-hunters have some inherent preferences and are more likely to harvest trees which appear to have large bee colonies which may contain more honey, but also prefer trees which are easier to cut down, meaning that some larger trees are avoided. In some cases, smaller trees are also not cut down because the expected honey reward is also likely to be smaller.

In the second section, I investigate the specific influence of human–honeyguide interactions on tree cutting. Specifically, honeyguides may influence the size and species of trees cut down for honey if they take honey-hunters to a different subset of trees with bees compared to those which honey-hunters find without the cooperation of honeyguides. This may arise if honeyguides find a different distribution of bees' nests owing to their capacity for flight, compared to that of humans whose search behaviour is restricted to the ground (Chapter 2). Alternatively, if honeyguides do not influence the effects of honey-hunting on tree ecology, then trees found with and without the assistance of honeyguides should not detectibly differ in characteristics such as size and species, or in their probability of being cut.

In the final section, I assess whether rates of tree cutting for honey around Mbamba village are sustainable, by drawing together three lines of evidence about how tree cutting for honey affects tree demographics. First, I present trends over time in (1) the number and (2) species of trees which were cut down, and (3) the size classes of tree cut down relative to distance to the village. If tree resources are becoming limited due to tree cutting for honey, then honey-hunters should shift over time from cutting down more preferred to less preferred species or size classes over time (a standard method used to assess sustainability in other contexts; López-Hoffman et al. 2016). As the proximity to the village creates a use-intensity gradient (Figure 5.2), I also test whether honey-hunters cut down less preferred trees close to the village, which would indicate that the tree resource is being depleted. Second, I compare the cutting preferences of honey-hunters to the background stem densities of the species affected by tree cutting, to assess whether cutting disproportionately affects some species more than expected based on their background occurrence. If honey-hunters cut down certain species at disproportionately high rates relative to their background stem densities, then tree cutting on these species might be unsustainable, and could be altering the species composition of the landscape. Alternatively, if tree cutting is sustainable, then rates of cutting should broadly mirror background stem densities. Last, I use demographic models of four tree species commonly cut down to assess whether the rates of recruitment into the size class of trees big enough to host bee colonies (and thus be potentially cut down) are sufficient to compensate for their loss due to cutting, and thus maintain a stable size class structure in the population. I run these models with different levels of tree cutting to assess whether a decline driven by honey-hunting is predicted under different potential future scenarios.

Figure 5.1. (A) Aerial photo of the landscape utilized by honey-hunters from Mbamba village, with a west-facing view up the Lugenda river. (B) Yao honey-hunters in the study area invariably use locally made axes for cutting down trees. (C) The strength of Yao axe handles is reportedly the major factor limiting honey-hunters' ability to cut some of the largest trees with bees. (D) A tree cut down to harvest honey as viewed from the air.

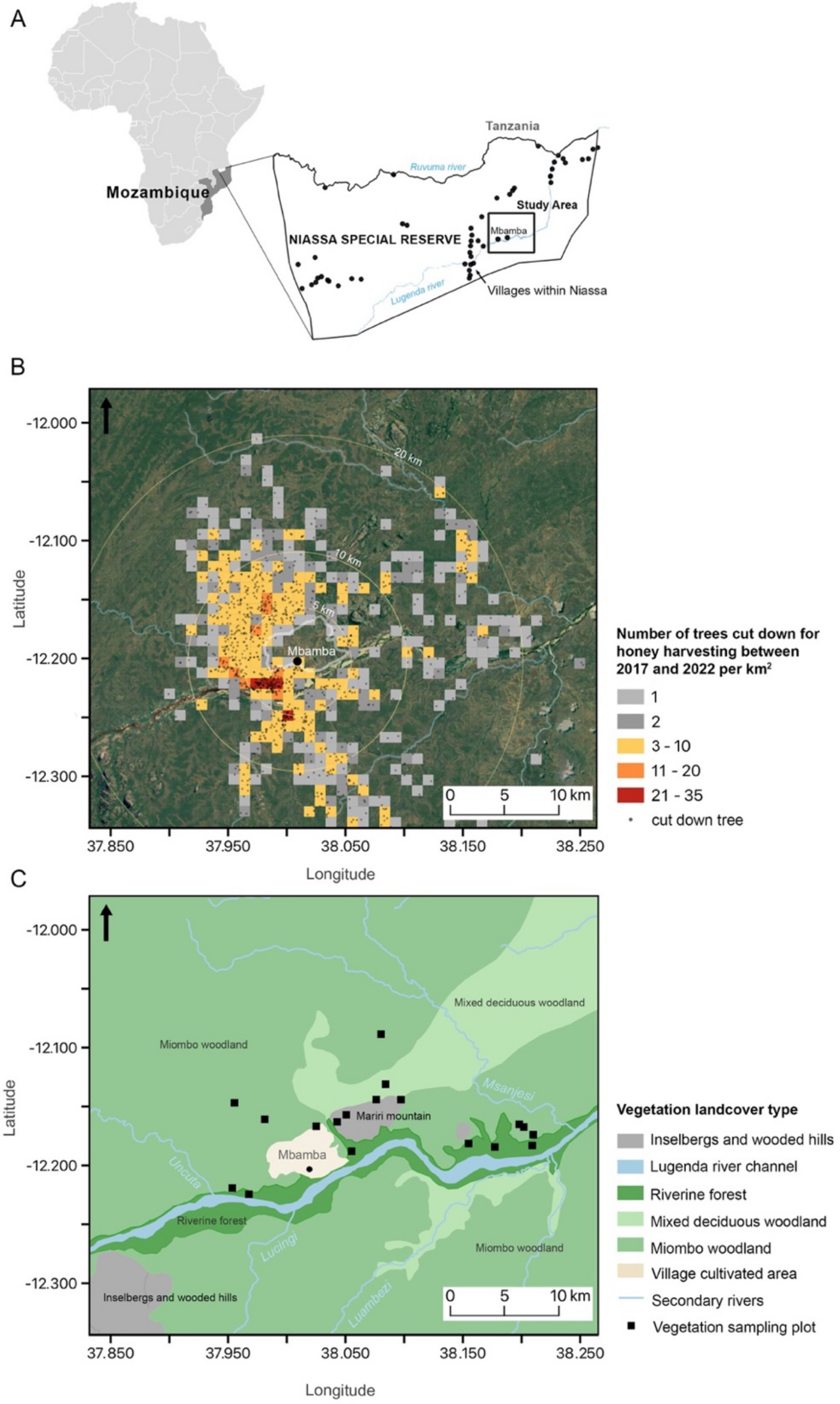


Figure 5.2. (A) Niassa Special Reserve is located in northern Mozambique, and our study area around Mbamba village to the southwest within it. (B) Tree cutting (the felling of above-ground biomass) due to honey harvesting occurs in a wide geographic area around Mbamba village. Between June 2017 and September 2022, twenty-one honey-hunters self-recorded data on 1,269 trees which they cut down to access honey, with areas nearest to the village and Lugenda River being most utilized. (C) Eighteen 0.25 ha tree demography plots were sampled across the three predominant vegetation types and across a range of honey-harvesting activity.

Methods

Study area

This study was carried out in a 627 km^2 area within Niassa Special Reserve, northern Mozambique (Figure 5.2). The entire study area is in range of Yao honey-hunters' foraging trips, usually originating from Mbamba village (12°12'S, 38°01'E) which has ca 2,000 inhabitants including > 30 regular honey-hunters (see Chapter 1 for further details).

The vegetation of Niassa has been classified as "drier Zambezian miombo woodland" (White 1983) which forms an important part of the miombo ecoregion (Timberlake et al. 2003). Throughout Niassa, tree diversity changes dramatically along the two large rivers (Lugenda and Ruvuma) and around granitic inselbergs. Overall, Niassa's vegetation can be broadly divided into five categories; (1) deciduous miombo woodland: these are distinctive well-grassed woodlands dominated by *Brachystegia* and *Julbernardia* species, occurring on relatively sandy nutrient-poor soils (Desmet 2004; Burrows et al. 2018), interspersed with hydromorphic grasslands (mbugas) with a frequent fire regime (Desmet 2004; Ribeiro et al. 2017); (2) lowland evergreen forests: small diverse areas of secondary growth, often with bamboo thickets (*Oxytenanthera abyssinica*) and usually located along the bases of steeper slopes; (3) riverine forest: these distinct lowland forest species assemblages are confined to alluvial soils and generally associated with the major rivers, forming narrow bands 20–600 m wide; (4) exposed dry forest: found only on granitic inselbergs and are moisture deficient and tend to be shrubby vegetation dominated by sedges, grasses, *Xerophyta* spp. and succulents; (5) evergreen moist forest: found only on Serra Mecula in small patches at higher elevations (1000–1300 m a.s.l.). In this chapter, the majority of data collection was conducted in a radius of 20 km around Mbamba village in miombo woodland or riverine habitat (Figure 5.1, 5.2).

Our study area has an elevation of 380–450 m above sea level and the climate is sub-humid tropical with mean minimum and maximum air temperatures ranging between 16–33°C in the dry season (May–October) and 22–32°C in the wet season (November–April). Rainfall begins in November and ends in late April or early May, and during this period precipitation averages 250–350 mm per month. Bees' honey stores, which build up throughout the rains with the flowering of dominant species, peak in May–June, deplete as the dry season progresses, and then usually peak again in November–December (sometimes January) following the flowering of trees prior to the following rainy season (Lawton 1982, pers. obs.).

Data collection

Three datasets were collected and used in this chapter (each described in detail below). First, twenty-one honey-hunters from Mbamba village used a custom application loaded on ruggedized smartphone (as in Chapter 2) to assist with collecting data on 5,293 trees hosting *Apis* and non-*Apis* bees over five years (June 2017 to September 2022). Second, I measured trees in eighteen 0.25 hectare (ha) vegetation sampling plots located across the study landscape. These data were collected from 3–23 June 2023. Last, I collected tree resprouting and survival metrics by re-visiting 79 harvested trees 1–5 years after they were harvested, and these data were collected from 4–16 December 2023.

Honey-hunter tree data. As in Chapter 2, our custom data collection system enabled a group of honey-hunters to self-collect data on their interactions with honeyguides and the trees they were guided to. Up to twenty-one honey-hunters at any one time (representing between a third to a half of all active honey-hunters from Mbamba village) collected data over 5 years and were selected based on my direct honey-hunting experience with them as well as guidance from the traditional chiefs of Mbamba village. Throughout this chapter, unless otherwise stated, 'current rates of cutting' refers to rates of cutting by this group during 2017–2022; i.e., approximately one third to half of the total rate of tree cutting activity by honey-hunters from Mbamba village, given that the 14–21 honey-hunters who collected data for this study are a subset of the total number of honey-hunters in Mbamba village (Chapter 2).

Our icon-driven application (designed by myself, Andrew Rayner of HabitatInfo, Wales, UK, and Claire Spottiswoode) contains a series of steps mimicking the natural progression of a honey-hunt and a variety of outcomes (see Chapter 2). For example, the icons for the following questions occur in this sequence: "Were you guided by a honeyguide?" [Yes], "What happened next? [found tree], "Did you harvest the honey?" [Yes], "Did you cut the tree down?" [Yes] (Appendix to Chapter 2). The icon-driven interface, also containing some widely understood Kiswahili words as prompts, proved to be highly compatible with low literacy rates. It was loaded and run on rugged handheld Android devices (Cedar CT5, Juniper Systems, Logan, Utah, USA) which featured accurate GPS capabilities.

When collecting data, the honey-hunters recorded all honeyguide and honey-harvest related events occurring during each foraging trip away from the village. If a tree with a *Apis, Melipona* or *Hypotrigona* bees' nest was found, its circumference in centimeters was measured at 1.3 m above the ground using a tape measure, and entered into the app. The tape measure was

300 cm long, and any tree with a CBH of > 300 cm (such as all baobabs *Adansonia digitata* and some *Sterculia* spp. individuals) was indicated as such using a dedicated button. Circumference values were converted to diameters using the formula *diameter = circumference/π* prior to all analyses. Also entered into the app were answers to prompts as to whether or not the tree was harvested for bees, and whether or not honey-hunters cut down the main stem in the process. All such events were sequentially stored with latitude/longitude coordinates and time. The completion of each step moved the user onto the following step, and the app was specifically designed to provide multiple naturally occurring options to the user at each decision-making point. If a mistake was made by clicking on the wrong icon or entering a value incorrectly, the user could go back to the previous step using the 'back button'. Each of these 'back button' presses was also recorded by the app as an event, greatly assisting subsequent reviews of data accuracy (see Chapter 2 for details). When recording the identification of trees and photographing bees' nests, the app required images and/or voice notes to be recorded and stored.

Five-second voice notes identifying the tree species containing bees were of particular importance. All honey-hunters were highly competent at identifying and assigning a local vernacular (Yao) name to each tree found (n = 205 species), and except for a few uncommon species (which I followed up on individually), there was a one-to-one match between Yao names and scientific names in a list which was developed and validated over 5 years of field work. Tree identification by Yao honey-hunters was remarkably accurate and consistent across the whole period of data collection, and for n = 70 trees which were recorded in the absence of a researcher and revisited in 2023, there was a 100% match between reported and observed tree species. Two sets of two species share Yao vernacular names ('Nangolwa' for *Philenoptera bussei* and *P. violacea*; and 'Ne'pa' for *Combretum collinum* and *Pteleopsis anisoptera*), so for these species we group records under the names *Philenoptera violacea* and *Combretum collinum* respectively. Data accuracy was verified for a subset of 500 trees by comparing the recorded species name with photographs of the tree, for which data were 100% accurate, leading to a high level of confidence in species identification. All 5-second voice notes identifying tree species were manually transcribed and matched to an index of scientific plant names.

All app-collected data were saved in SQL databases and copied from the devices periodically (initially monthly, later twice a year) and reviewed in R (R Core Team, 2023), primarily using a custom R Shiny application developed by Brian M. Wood. This interface mapped honey-hunting trips, events and images alongside tabular data, allowing the visual inspection of each event or trip to be spatially checked against categorical data, while integrating data 'reviews' back into the SQL databases. All honey-hunting trips and 'events' were reviewed in systematic way using a carefully defined set of rules to remove unintentional records, training trips and other inconsistencies (Appendix to Chapter 2). Data collection was carried out with full informed consent and received approval from the University of Cape Town Faculty of Science Research Ethics Committee (approval number FSREC 22–2017).

Tree plot data. For background vegetation data on trees not containing bees, I set up 18 sampling plots which were semi-randomly located, with reasonable accessibility and good representation of the area utilized by honey-hunters and of the range of land cover types (*mixed deciduous woodland*, *miombo woodland* or *riverine forest*), with six plots in each vegetation type (Figure 5.2C). These data were collected using a standardised tree plot measurement protocol for African woodlands and savannahs (SEOSAW; Socio-Ecological Observatory for Studying African Woodlands, https://seosaw.github.io/manuals.html). From 18 starting points, together with 1–3 Yao field assistants (Carvalho Issa Nanguar, Seliano Rucunua, Fatima Balasani), I walked 100 m at a random bearing then laid out a 50 x 50 m plot in which every tree stem > 10 cm circumference (later converted to diameter at breast height, 'DBH', i.e., ~3 cm diameter) was measured at 1.3 m above ground level. I either identified tree species directly, or trees were identified by one or more field assistants to a local vernacular name which was matched to its scientific name. For each stem I recorded whether the tree was alive, whether it was standing, multi-stemmed, damaged or not, and the cause of damage (elephants, termites, fire, humans, wind, animals not elephants) where it could be determined.

To stratify the vegetation plots (Figure 5.2C), I mapped the three broad habitat types in the study area. These were: (1) *mixed deciduous woodland*, known to the honey-hunters as 'maputi' and characterised by a mixed savannah tree assemblage dominated by species such as *Millettia stuhlmannii*, *Acacia nigrescens, Albizia amara, Sclerocarya birrea, Afzelia quanzensis* and *Lannea schweinfurthii*; (2) *miombo woodland*, known to the honey-hunters as 'ndando' and characterised by species such as *Julbernardia globiflora*, *Brachystegia boehmi*, *Terminalia stenostachya*, *Erythrophleum africanum, Pterocarpus angolensis, Pseudolachnostylis maprouneifolia* and *Diospyros kirkii*; and (3) *riverine forest,* also known to the honey-hunters as 'maputi' but consisting of a distinctive species assemblage including larger species such as *Adansonia digitata, Acacia rovumae, Ficus bussei, Sterculia appendiculata* and *Kigelia africana,* and occurring within 300 m of major drainage lines or rivers. The boundaries of these three vegetation classifications were broadly determined from 1,500 georeferenced tree records (from the same 2017–2023 dataset as used elsewhere in this chapter), Philip G. Desmet's Niassa vegetation survey (Desmet 2004), and satellite imagery (ESRI 2023).

Resprout data. This comprised data on 70 trees of multiple species with *Apis* bees previous harvested by honey-hunters between in 2017 and 2022 and revisited in December 2023. For each of the stems I recorded whether the tree had resprouted, and if it had, counted the number of shoots from either the base of the tree or the stem (stump). I also verified the tree species identifications made by honey-hunters using the app. For four species, I used these data to parameterize post-cutting resprout rates in a demographic model.

Statistical analysis

To visualize spatial patterns of honey harvesting around Mbamba village, I mapped cut down trees and vegetation habitat types using QGIS version 3.30 (QGIS development team 2023). I conducted all statistical analyses using R version 4.3.0 (R Core Team, 2024). Although trees with honeybees (*Apis*) formed most bee tree records (65%, n = 3,472 of 5,293 tree records) for the purposes of assessing the impact of tree cutting, I include all cut trees found with *Apis* and non-*Apis* species (*Melipona* or *Hypotrigona*), unless stated otherwise. Trees that were harvested but not felled (i.e., cut *into* but not cut *down*) are included in bee and honey-hunter preference analyses, but not included when calculating rates of stem cutting or likelihood of tree being cut down, or considered in the demographic model.

To compare the size classes and species found with bees and cut down, relative to their availability in the landscape, I produced density plots by size (DBH) for i) stems with bees, ii) stems cut down by honey-hunters and iii) the background stem densities (all > 3 cm DBH; Figure 5.4). Background densities were determined using data from the 18 vegetation plots (Figure 5.2), whereas densities of trees found with bees and cut down were measured across the whole landscape over 5 years. Rare species, and species that are associated with specific habitats were not well represented in the 18 vegetation plots, so I did this only for species for which I had good background density data (hereafter, 'major species'): *Julbernardia globiflora, Terminalia stenostachya, Albizia amara, Millettia stuhlmannii, Combretum collinum, Sclerocarya birrea, Combretum adenogonium, Pterocarpus angolensis, Brachystegia boehmi, Pseudolachnostylis maprouneifolia, Terminalia sambesiaca, Brachystegia spiciformis, Diospyros kirkii* and *Philenoptera bussei* (shaded rows in Table 5.3). To assess the fate of the cut trees, I used the dataset of 70 bee trees that I surveyed in December 2023 and assessed the probability of resprouting after a harvesting event.

To compare the ranking of tree species 'preferred' by bees and those 'preferred' by honey-hunters for cutting down, I calculated the relative abundance of tree species associated with bees as: $n_i / \Sigma n$, where n_i represents the number of individuals of species i found with bees, and Σn is the total number of trees found with bees. Similarly, the relative abundance of trees 'preferred' by honey-hunters was calculated as: $c_i / \Sigma c$ where c_i is the number of individuals of species i cut down by honey-hunters, and Σc is the total number of trees cut down (Table 5.4). This was calculated for all 63 tree species in the honey-hunter dataset. I compared this with the 'background' relative abundances for all 63 species based on stem counts in the 18 vegetation sampling plots (relative % of total stems > 10 cm DBH/ha) (Table 5.3). I excluded baobabs *Adansonia digitata* because this species was never cut down (Table 5.3).

To assess how selective honey-hunters are when deciding whether to harvest, I tested whether tree species and size determine the probability of bee-trees being cut down. I ran generalized linear mixed-effects (GLMM) models fitted using the 'glmer' function in the *lme4* package in R (Bates et al. 2015), and sequentially added predictors to a null model to determine whether they improve the explanatory power (using the ANOVA function and comparing the AIC values). The first model is the null (Table 5.2, model 1) with the probability of being 'cut' or 'not cut' as the binomial response and tree species (for the 14 species listed above) as the random effect. The second model (Table 5.2, model 2) was the same, but with tree size (DBH) as a linear fixed effect (testing whether, of the bee trees available, hunters were more likely to cut larger/smaller trees). I then tested whether the relationship between tree size and probability of being cut down was non-linear (i.e. whether there was a preferred range of size classes) by comparing model 2 (Table 5.2) against the same model but with a quadratic term for tree size (Table 5.2, model 3) (Burnham and Anderson 2002). I also tested whether the size classes that were cut differed by species by comparing model 3 with a similar logistic regression that included with a species–size interaction term (Table 5.2, model 4).

In part two of this study, I hypothesize that honeyguides take honey-hunters to a different subset of trees with bees than those which honey-hunters find without the cooperation of honeyguides, thus altering which trees are cut. To test this, I first used the same logistic regression model structure as previously, with 'cut' or 'not cut' as the binary response variable, DBH as a continuous predictor, and 'guided' or 'not guided' by honeyguides as a categorical predictor to test whether finding a tree with a honeyguide predicts the probability of a tree being cut down, and tree species as a random effect (Table 5.2, model 5). I then repeated this model with the inclusion of an interaction term between tree size and whether it was located with a honeyguide (Table 5.2, model 6).

I then tested whether the overall mean size of trees cut down differed when they were found with a honeyguide compared to found without a honeyguide, by running a Wilcoxon rank-sum test with DBH as the response variable and 'guided' or 'not guided' as the predictor variable (Wilcoxon 1945). Lastly, because honeyguides can fly and so may be able to locate a different subset of trees with bees to those found by humans, I use a Chi-squared test of independence to test whether trees found with the cooperation of a honeyguide were more likely to have a bees' nest located over 2 m above ground, compared to those found without the cooperation of a honeyguide. I also compared the overall diversity of tree species with bees to those found only with honeyguides, using the Simpson diversity index which measures the probability that two individuals randomly selected from a sample will belong to different species, using the *vegan* package in R. Using the same package, I also calculated the Shannon-Wiener index, which combines species richness and species evenness (which describes the distribution of individuals across the different groups).

In the final section, I draw together three lines of evidence to assess whether rates of tree cutting for honey around Mbamba village are sustainable. First, to test whether honey-hunters have shifted from cutting down more preferred to less preferred species or size classes over time, I calculated trends over time in the number of trees (for the major species) cut down for honey between 2017 and 2022. This time frame is likely too short to show an effect, but is included in the chapter because trends over such a short time scale would indicate rapid change. I adjusted the number of bee trees found annually for varying search effort by multiplying the observed counts by the relative difference in honey-hunting days between that year and 2019 (which was the busiest honey-hunting year, with 447 honey-hunter foraging days), to account for variation between years in the number of data collectors and their honey-hunting efforts. I then tested for trends in the number of bee trees found yearly by fitting generalized linear models (GLM) for each of the major species, with count as the response variable and year as the predictor.

To test whether tree cutting is unsustainable, I compared the size of trees cut near the village (high cutting rates) with those further away (low cutting rates). I made use of a gradient of harvesting intensity related to distance to village (an order of magnitude difference number of trees cut close to the village vs far; Figure 5.2B). If harvesting is depleting trees, then the availability of preferred stems should be lower closer to the village, and honey-hunters should therefore cut down less-preferred size classes close to the village. I tested this by fitting a general linear regression using the package *lme4*, with distance to village as the response variable, tree DBH as the predictor, and species as a random effect. The significance of the fixed effects was tested against a null model using likelihood ratio tests with the Kenward-Roger approximation for degrees of freedom, implemented via the *pbkrtest* package.

Lastly, I developed a demographic model for four species (*Julbernardia globiflora*, *Terminalia stenostachya, Pterocarpus angolensis* and *Combretum adenogonium*), selected because they are four of the most cut down species and have good demographic information. I ran 1,000 simulations of the model for each species under different harvesting rates (current, 10x current, and 100x current). The model and its parametrization are described separately below (Table 5.1, Figure 5.3).

Table 5.1. Demographic model parameters used to simulate changes in stem densities due to varying levels of tree cutting due to honey-hunting activity. The model simulates the transition in the number of stems (per km^2), across a total woodland area of 420 km^2, between the gulliver (< 3 cm DBH size class and set here for consistency at 5,000 stems/km^2), sapling, bee tree and elder size classes (each varying by species) (Figure 5.3).

Species	Size class (DBH cm)	Density (stems/km^2)	$_p$(mortality) (max, min)	$_p$topkill	Max growth rate (cm/yr)	$_p$cut	$_p$resprout	$_p$re-seeding	Self-thinning term	Carrying capacity (stems larger than gulliver /km^2)
Julbernardia globiflora					0.3*		0.01	0.01	0.05	2000
gulliver	0–3	5000	0.01	0.05						
sapling	3–25	1244	0.05–0.01	0.99						
bee tree	25–53	622	0.02–0.005	0.99		0.0002				
elder	53–81	32	0.02 – 0.01							
Terminalia stenostachya					0.14*		0.01	0.01	0.05	5100
gulliver	0–3	5000	0.01	0.05						
sapling	3–19	4044	0.05–0.01	0.99						
bee tree	19–56	822	0.02–0.005	0.99		0.0001				
elder	56–73	1	0.02 – 0.01							
Pterocarpus angolensis					0.26*		0.01	0.01	0.05	1000
gulliver	0–3	5000	0.01	0.05						
sapling	3–28	822	0.05–0.01	0.99						
bee tree	28–65	66	0.02–0.005	0.99		0.0006				
elder	65–95	2	0.02 – 0.01							
Combretum adenogonium					0.15*		0.05	0.01	0.05	3000
gulliver	0–3	5000	0.01	0.05						
sapling	3–25	2555	0.05–0.01	0.99						
bee tree	25–57	177	0.02–0.005	0.99		0.0005				
elder	57–84	5	0.02 – 0.01							

* growth rates (DBH cm/yr) for these species, which are widespread across Africa, were parameterized using data from Kilwa, south-eastern Tanzania, in comparable habitat approximately 380 km from our study site (Bowers 2017) and compared for realism to Ribeiro et al. (2017).

A demographic model of change in tree stems densities with various cutting rates

Demographic models simulating the population dynamics of tree species are a common method in ecology and forestry to estimate levels of sustainable offtake or harvest (Caswell 2001). Here, I use a matrix model-type framework (see Baxter and Getz 2005, Twine and Holdo 2016) to simulate the upward transitions of stems across various tree size classes and forecast stem counts per square kilometre over 100 years.

For my model, I first defined four tree size classes: first, 'gullivers' (see Box 1), referring to small stems which are larger than recently germinated seedlings but less than 3 cm DBH, and still occur within the fire trap (a cycle of above-ground biomass loss following resprouting due to fire; Bond 2008). Gullivers transition into 'saplings', which range from 3 cm DBH to up a DBH which varies by species and reflects the threshold at which a tree is large enough (values derived directly from observed data Table 5.1.) to host *Apis*, *Melipona*, or *Hypotrigona* bee species, and therefore is at risk of being cut down by a honey-hunter. After growing large enough to host bees, a sapling becomes part of the 'bee tree' size class, which is the class of particular interest here. Finally, once a bee tree stem is bigger than the size at which a honey-hunter is willing to cut it down (threshold derived directly from the observed data; Table 5.1), the stem enters the 'elder' size class and remains in this size class, leaving only due to the background rates of mortality (Figure 5.3).

The relevant size class boundaries for four frequently preferred bee tree species (*Julbernardia globiflora*, *Terminalia stenostachya, Pterocarpus angolensis* and *Combretum adenogonium*) were determined using honey-hunter collected data for 5th and 95th percentile DBHs of trees cut down for honey (Table 5.3), and the gulliver to sapling boundary was determined from the literature (Bowers 2017). This model assumes that the trees in this ecosystem are recruitment limited, not establishment limited (Bond et al. 2017, Holdo et al. 2014), and that a stock of juvenile plants is always available to replace adult stems from the population. This is a reasonable assumption for trees that are clonal (e.g. *Julbernardia*), and for *Terminalia stenostachya, Pterocarpus angolensis* and *Combretum adenogonium,* which are not thought to be clonal, this assumption is supported by the large numbers of juvenile trees of these species within the study area. I therefore set initial gulliver stem densities to 5,000 stems per kilometer squared (Table 5.1) to ensure that this size class is never depleted. For the sapling, bee tree and elder size classes, I determined the baseline stem densities (Table 5.1) using direct stem counts in the sampling plots (multiplied to obtain square kilometer densities).

Top-kill occurs when tree stems lose all their above-ground biomass due to disturbances such as fire, elephants (*Loxodonta africana*), termites, and human harvesting (Ribeiro 2017), but due to their ability to resprout, are not killed, but rather return to smaller size classes in the population. By contrast, mortality occurs when stems die, fail to resprout and are lost from the population (see Box 1). For each size class, I defined a mortality rate from Bowers (2017), and to account for interannual variation in probability of death I set these mortality values to vary stochastically within the model (drawn from a normal distribution using the R function 'rnorm'), across a range of realistic values from year to year. Top-kill by fire, elephants or termites was represented by a top-kill probability ($_p$topkill): for the saplings, bee trees, and elders this represented the proportion of trees that were returned to the gulliver class at each timestep. For the gulliver size class this represented the proportion of stems that stayed in the gulliver class and which did not progress to the sapling class each timestep.

By using proportions instead of absolute numbers, I ensure that the top-kill and cutting rates go down as the availability of trees declines. This is a weak assumption for cutting effects, and possibly for elephant damage, but is likely to be valid for fire damage. In the model, stems across all size classes were subject to average annual increases in DBH (cm), which yearly transitioned some stems out of each size class into the next. Values used here for growth rates were taken from measurements made under similar climatic conditions and species community structure (Bowers 2017, Ribeiro et al. 2017).

The modelled tree cutting term (i.e., probability of a given stem being cut down by honey-hunters) is a variable (p^{cut}) which only influenced the bee tree size class. Cutting rates were fixed values (Table 5.1) derived separately for each tree species by taking the mean number of bee trees cut down per year, divided by the estimated total available number of stems available for that species over the 420 km^2 honey-hunting foraging area. The total available stems estimate was derived from counts made in the vegetation sampling plots. Cutting rates were not calculated separately for each habitat type because the mean rates appeared to be realistic for across the whole study area. The central test of the long-term impact of tree cutting was to run the models with three levels of cutting: 1) the present observed rate, 2) 10 times the present rate and 3) 100 times the present rate.

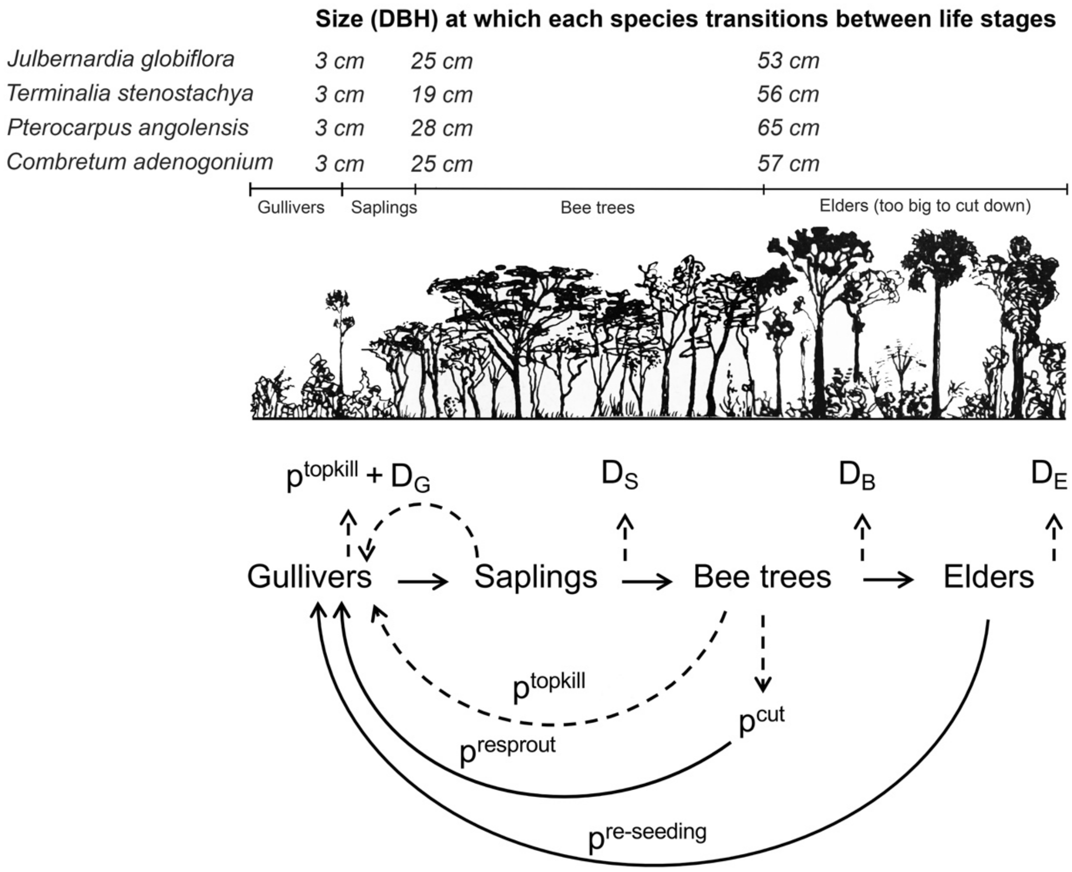


Figure 5.3. The sizes (DBH) at which four tree species transition between size classes, along with a diagram of the modelled demographic process. In this model, trees sprout and become 'gullivers', which have a rate of top-kill from fire ($p^{topkill}$) or die at a background mortality rate (D_G). Gullivers transition to saplings which also have background mortality (D_S), and if they survive to grow large enough to host a bee colony, enter the 'bee tree' stage. Some bee trees are cut down by honey-hunters (p^{cut}) and some of these cut down trees resprout or coppice ($p^{resprout}$). Bee trees also have a background mortality rate (D_B), but if they survive beyond the size at which a honey-hunter will cut down these trees, they transition to the 'elder' stage where they are largely safe from honey-hunter's axes but have a higher natural mortality rate (D_E).

A $_{p}$resprout (coppicing) term was included following the cutting of a tree. This value is the probability that a cut down stem, for a given species, resprouts and therefore contributes back to the gulliver class (Chidumayo 2004; Twine and Holdo 2016). The yearly proportion of resprouts (Table 5.2) was based on the mean observed rate of resprouting at previously cut down trees which were revisited in 2023, pooling all species (n = 70). In a future version of this model, resprout rates per species can be refined further with more data collection or from the literature, but here are set currently to a realistic mean based on field observations.

Trees within the ‘elder’ size class play an important ecological role as a source of seeds back into the ecosystem, and because fruiting increased exponentially with tree stem diameter most seeds are produced by the largest trees. In this model, I account for the disproportional impact that the removal of a few larger stems could have by including a reseeding rate term into the model. The $_p$reseeding term is the proportional contribution which elders make to the seedling counts on a yearly basis (e.g., Twine and Holdo 2016).

Lastly, I account for density-dependent effects on population growth by using a self-thinning term in the model. This term decelerates the number of stems transitioning from gulliver to sapling as the count approaches the maximum that the habitat can support (Baxter and Getz 2005, Twine and Holdo 2016). Specifically, the model adjusts growth rate based on the total number of sapling, bee tree, and elder stems relative to the carrying capacity, with growth rate reducing as the total number of stems approaches carrying capacity. Carrying capacity values (Table 5.2) are set with the assumption that observed total density of stems in this landscape is stable over at least a 100-year timeframe, based on currently observed number of trees in the landscape. This assumption is supported by empirical values from plot data, which are consistent with the carrying capacities of similar areas of miombo woodland (e.g., Montfort et al. 2021). For the three levels of cutting, I ran 1,000 model simulations to incorporate inter-year variability. I plotted the mean outcomes for the 1,000 simulations with 95 percent confidence intervals for projected stem densities for 100 years.

Results

Spatial patterns of tree cutting

Tree cutting due to honey-hunting was recorded in an area of 420 km^2 around Mbamba village (Figure 5.2). Trees were cut down to harvest honey up to 30 km from the village, yet the areas of highest cutting rate (measured over 5 years) occurred at 4–7 km from the village, and relatively close to the perennial water source of the Lugenda river (Figure 5.2). The highest recorded density of cut down trees was 35 stems in one square km over 5 years, but for 64% of the area only 1 or 2 stems/km^2 were cut down, and these low-impact areas tended to be > 5 km from Mbamba village (21.7 % of all cut trees were within 5 km from the village). A similar number of trees was cut on the southern side of the Lugenda river as on the northern side, despite the flooding of the Lugenda river over the wet season (January–April) presenting a significant barrier to resident honey-hunters on its northern bank (Figure 5.1A). The overall pattern of honey-hunting and tree cutting activity radiated outwards from Mbamba village, particularly stretching east along the Lugenda river where many honey-hunters also fish seasonally, and also along the Msanjesi river where specific honey-hunting trips were made to access areas of low honey-hunting activity (Figure 5.2).

Trees species and sizes preferred by bees

Of the 162 tree species recorded in the area, bees were found in 63 species: 60 with *Apis* bees, 35 with *Melipona* stingless bees and 44 with *Hypotrigona* stingless bees (Table 5.3). Generally, across all tree species, bees tended to occupy the larger stems of each species (Figure 5.4). Bee-occupied trees spanned from 8 cm DBH to > 95 cm DBH (in the case of *Sterculia* species and baobabs, *Adansonia digitata*). Three notably large tree species, *Millettia stuhlmannii, Sclerocarya birrea* and *Albizia amara*, were regularly occupied by bees and in some cases cut down (Figure 5.5, 5.6).

Honey-hunter tree cutting preferences

Less than half (38.8%) of the trees found with bees were harvested for honey, showing strong honey-hunter preference. Rates of cutting varied widely between species (Table 5.3): honey-hunters cut 59%, 57%, and 56% respectively of the *Terminalia stenostachya, Julbernardia globiflora*, and *Combretum adenogonium* bee trees, but only 9% of the *Acacia nigrescens* and *A. rovumae* bee trees, despite these being commonly found (Figure 5.5, Table 5.3). Large tree species (e.g. *Sterculia appendiculata, Adansonia digitata*) were rarely or never cut down (Table 5.3).

Smaller trees were more likely to be harvested, with tree size significantly improving the explanatory power of a model predicting likelihood of whether a tree with bees would be cut down ($\chi^2 = 78.5$, df = 1, $p < 0.0001$; Table 5.2). There was no evidence for improved fit with a square term (Table 5.2, model 2), indicating that the relationship between DBH and probability of being cut down is near-linear (AIC value of 3152 is identical between linear and nonlinear models; Table 5.2). Some species escape cutting (i.e., outgrow the size range which honey-hunters prefer to harvest) at a smaller DBH than others, indicated by the model being significantly improved ($\chi^2 = 11.5$, df = 2, $p = 0.003$) by the inclusion of a random slope (where the response to DBH varied by species). Although harvested trees were generally smaller than those which were not cut down (Figure 5.6A, Figure 5.5), certain species (e.g., *Pseudolachnostylis maprouneifolia*) appear not to have a maximum size threshold (i.e., they never escape harvesting).

Table 5.2. Generalized linear mixed models (GLMMs) used to evaluate the relationship between the probability of a tree being cut down and tree size, tree species, and whether it was located with the cooperation of a honeyguide, with corresponding AIC values and coefficients.

Model	Testing whether	Model	AIC
1	Species predicts probability of being cut down	$_{p}$cut down ~ 1 + (1| tree species)	3229
2	Tree size predicts probability of being cut down (tree species as a random effect)	$_{p}$cut down ~ tree size + (1| tree species)	3152
3	The relationship between tree size and probability of being cut down is non-linear	$_{p}$cut down ~ tree size + tree size * tree size + (1| tree species)	3152
4	The size classes of trees that are cut down depends on species	$_{p}$cut down ~ tree size + (size | species)	3144
5	Tree size and whether or not it was located with a honeyguide (guided) predicts the probability of a tree being cut down (tree species as a random effect)	$_{p}$cut down ~ tree size + guided + (1| species	3084
6	Tree size and whether or not it was located with a honeyguide (guided) interact to predict the probability of a tree being cut down (tree species as a random effect)	$_{p}$cut down ~ tree size * guided + (1| species)	3081

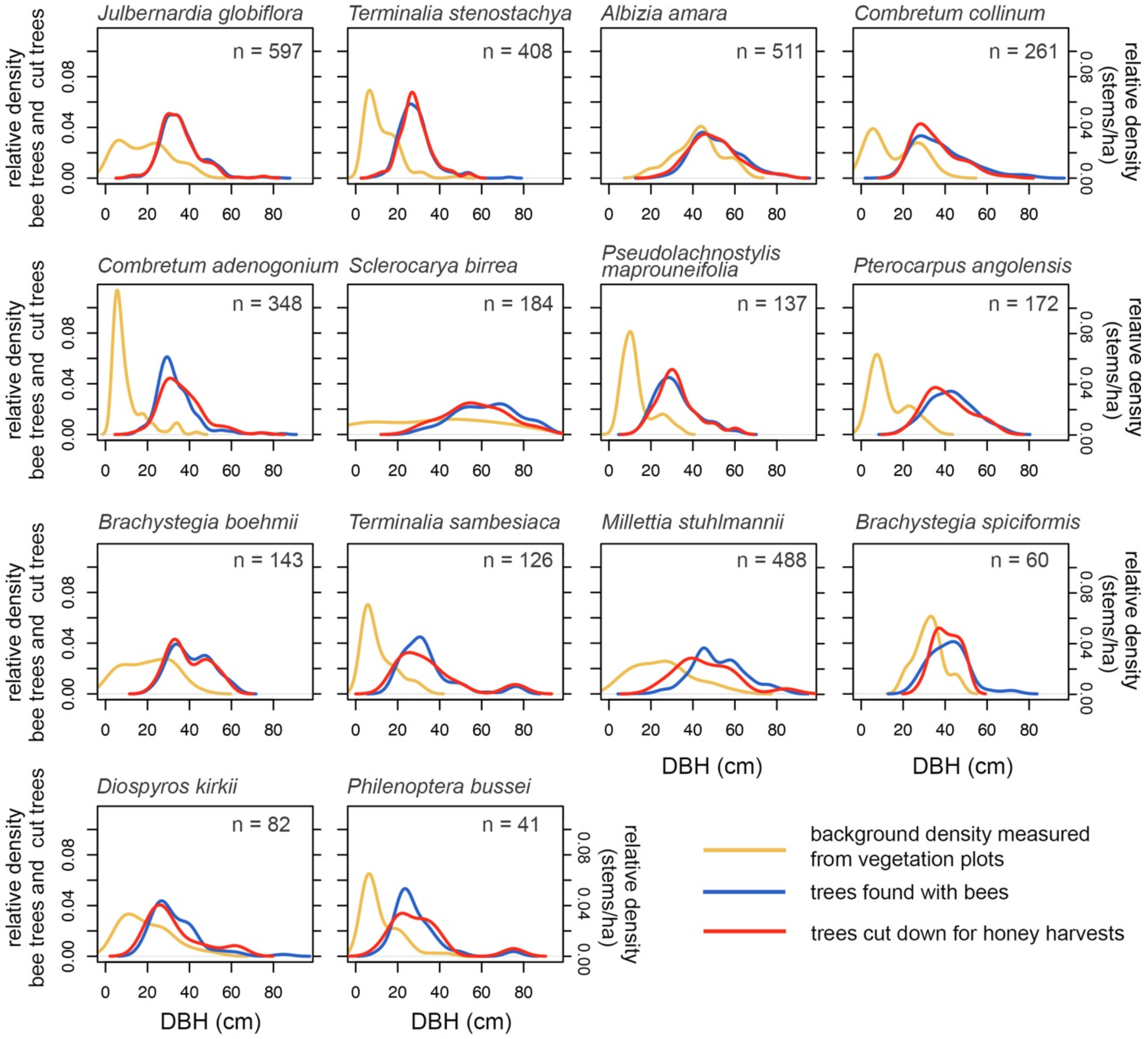


Figure 5.4. Tree species preferred by bees and those preferred by honey-hunters for cutting do not always reflect the trees available for occupation by bees in the environment. Here the relative densities (proportion of total trees recorded), by size (DBH), of all trees found with bees (blue lines), trees cut down (red lines) and the background stem densities per ha (yellow lines; all stems > 3 cm DBH) are plotted for fourteen major tree species. Note the different spatial scales: cut and bee tree densities are for the full landscape over 5 years whereas background relative densities (yellow lines) were measured across 18 vegetation plots (Figure 5.2C).

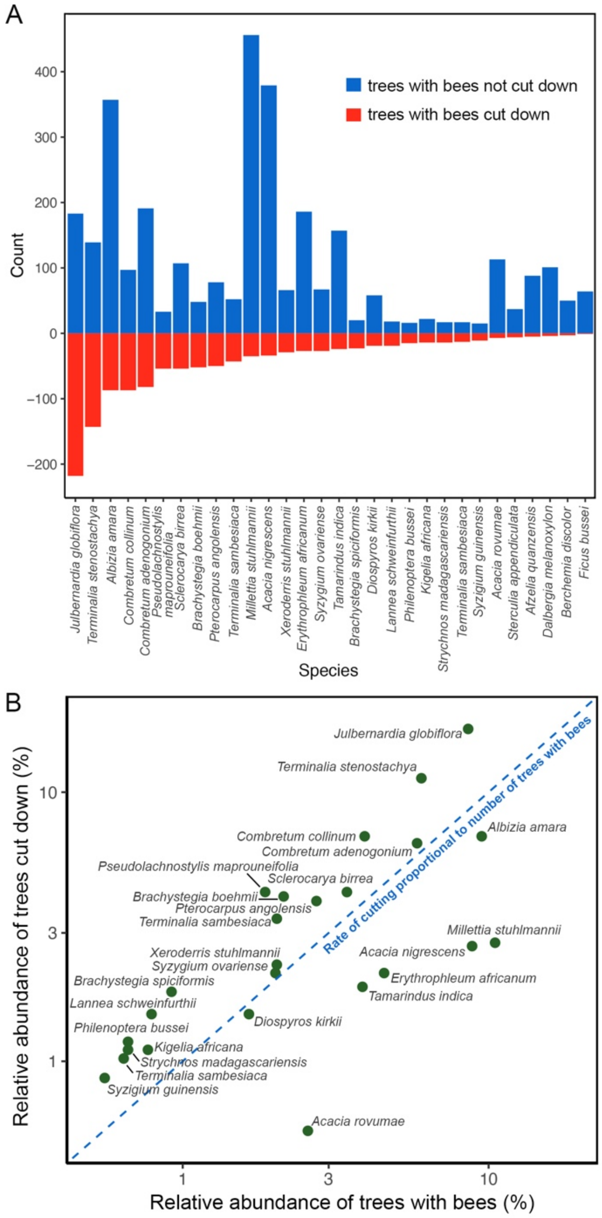


Figure 5.5. Tree species preference varies for bees and for honey-hunters. (A) Bar plot showing the number of trees, by species, which were found with bees but not cut down (blue bars) and cut down for honey harvests (red bars). Species with larger red than blue bars were 'preferred', and species with larger blue than red bars were 'avoided' by honey-hunters. For values of the proportion of available bee trees that were cut, see Table 5.3. (B) Plot of the relationship between bee tree relative abundance (% of total number of stems recorded with bees) and preference by honey-hunters for cutting down (% of total bee tree stems cut down). Species towards the top left are most cut down relative to availability, and those in the bottom right least cut down relative to availability.

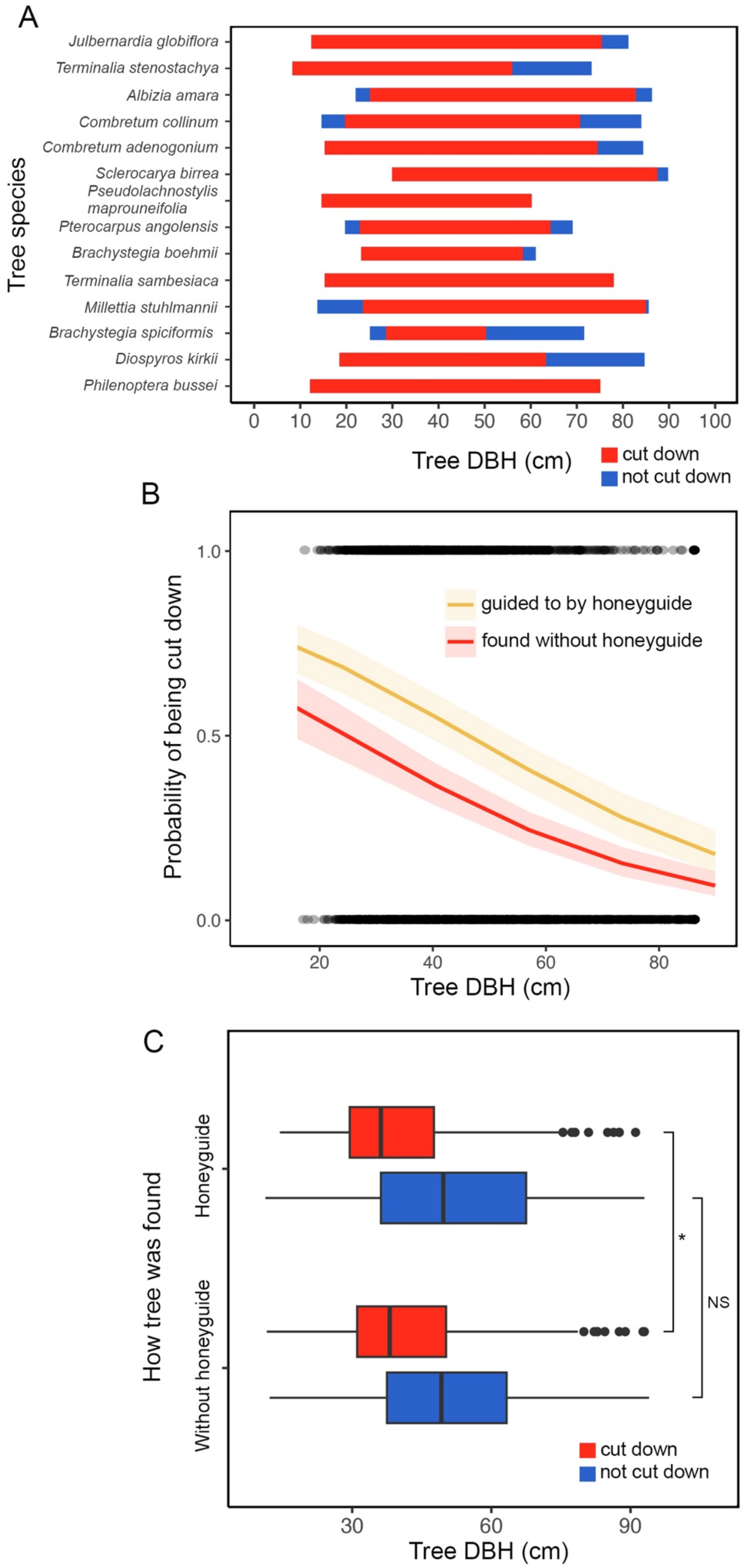

A
Tree species
Julbernardia globiflora
Terminalia stenostachya
Albizia amara
Combretum collinum
Combretum adenogonium
Sclerocarya birrea
Pseudolachnostylis maprouneifolia
Pterocarpus angolensis
Brachystegia boehmii
Terminalia sambesiaca
Millettia stuhlmannii
Brachystegia spiciformis
Diospyros kirkii
Philenoptera bussei
0
10
20
30
40
50
60
70
80
90
100
Tree DBH (cm)
🟥 cut down
🟦 not cut down
B
Probability of being cut down
1.0
0.5
0.0
guided to by honeyguide
found without honeyguide
20
40
60
80
Tree DBH (cm)
C
How tree was found
Honeyguide
Without honeyguide
*
NS
🟥 cut down
🟦 not cut down
30
60
90
Tree DBH (cm)

Figure 5.6. (A) In the fourteen of tree species most commonly found containing bees' nests (ordered by most frequently cut down at the top), those which honey-hunters choose to cut down (red) tend to be smaller than those which they found overall (blue), yet for some tree species honey-hunters cut down any sized tree found with bees, even those with large stems. (B) The probability that a tree with bees will be cut down is negatively correlated with the size of the tree (i.e., the larger the tree the less likely it is to be cut down) and trees found with honeyguides are more likely to be cut down. Predicted curves are derived from model 5 (Table 5.2). (C) Honeyguides also influence the average size of tree which get cut down, because trees with *Apis* bees found with the help of honeyguides tend to be slightly smaller (39.6 ± 0.57 cm DBH, mean ± SE) than those found without honeyguides (41.8 ± 0.67 cm DBH, mean ± SE) (Wilcoxon rank sum test results: $Z = 4.86$, $p = 0.015$, $n_1 = 552$, $n_2 = 489$).

Table 5.3. Tree species occupied by three types of bee (*Apis mellifera*, *Melipona* stingless bees, and smaller *Hypotrigona* stingless bees) recorded in an area of 420 km^2 around Mbamba village, Niassa Special Reserve. For each tree species found with bees, the 5th and 95th diameter at breast height (DBH) is reported; for some larger tree species (>100 cm DBH), Yao honey-hunting data collectors did not record the exact size. The fourteen focal species used to compare tree cutting to background stem densities are shaded. Species in bold are those included in the demographic model.

	Diameter at breast height (cm)		***Apis* bees**		***Melipona* bees**		***Hypotrigona* bees**	
Tree species	**5th percentile**	**95th percentile**	**Total trees found with bees**	**Cut trees (%)***	**Total trees found with bees**	**Cut trees (%)**	**Total trees found with bees**	**Cut trees (%)**
Adansonia digitata	>100	>100	565†	0 (0%)	13	0 (0%)	37	0 (0%)
Julbernardia globiflora	25	53	344	197 (57%)	15	10 (67%)	42	11 (26%)
Acacia nigrescens	37	>100	258	24 (9%)	30	2 (7%)	125	8 (6%)
Terminalia stenostachya	19	46	199	117 (59%)	6	2 (33%)	77	24 (31%)
Albizia amara	37	80	184	61 (33%)	38	3 (8%)	222	23 (10%)
Millettia stuhlmannii	35	>100	180	25 (14%)	83	5 (6%)	228	5 (2%)
Combretum collinum	23	64	164	83 (51%)	7	4 (57%)	13	0 (0%)
Tamarindus indica	40	>100	160	23 (14%)	6	0 (0%)	15	1 (7%)
Sclerocarya birrea	41	>100	152	53 (35%)	3	1 (33%)	6	0 (0%)
Combretum adenogonium	25	57	135	75 (56%)	22	3 (14%)	116	4 (3%)
Pterocarpus angolensis	28	63	92	45 (49%)	7	1 (14%)	29	4 (14%)
Brachystegia boehmii	29	57	87	49 (56%)	6	2 (33%)	7	1 (14%)
Pseudolachnostylis maprouneifolia	19	50	85	53 (62%)	0		2	1 (50%)
Acacia rovumae	38	>100	76	7 (9%)	7	0 (0%)	37	0 (0%)
Afzelia quanzensis	42	>100	74	5 (7%)	4	0 0%)	15	0 (0%)
Terminalia sambesiaca	20	78	74	40 (54%)	1	0 (0%)	20	3 (15%)
Syzygium ovariense	30	83	71	25 (35%)	2	0 (0%)	21	2 (10%)
Ficus bussei	96	>100	57	1 (2%)	4	0 (0%)	4	0 (0%)
Erythrophleum africanum	25	68	53	18 (34%)	17	2 (12%)	143	7 (5%)
Brachystegia spiciformis	29	51	40	22 (55%)	1	1 (100%)	2	0 (0%)
Sterculia appendiculata	43	>100	40	5 (12%)	0		3	1 (33%)
Xeroderris stuhlmannii	32	73	36	20 (56%)	17	4 (24%)	42	5 (12%)
Lannea schweinfurthii	34	71	30	18 (60%)	1	0 (0%)	6	1 (17%)
Kigelia africana	29	92	28	12 (43%)	3	1 (33%)	5	1 (20%)
Diospyros kirkii	21	63	25	8 (32%)	2	0 (0%)	50	11 (22%)
Strychnos madagascariensis	22	58	25	13 (52%)	0		6	1 (17%)
Terminalia sericea	24	36	20	11 (55%)	0		10	2 (20%)

Piliostigma thonningii	38	62	19	11 (58%)	0		0	
Sterculia quinqueloba	45	>100	19	4 (21%)	0		2	0 (0%)
Sterculia africana	77	>100	18	1 (6%)	0		2	1 (50%)
Schinziophyton rautanenii	37	>100	15	2 (13%)	0		0	
Xylia torreana	53	90	15	5 (33%)	0		0	
Markhamia obtusifolia	17	45	14	10 (71%)	0		0	
Syzigium guinensis	13	>100	13	4 (31%)	3	2 (67%)	10	5 (50%)
Berchemia discolor	38	79	12	3 (25%)	11	0 (0%)	30	0 (0%)
Philenoptera bussei	22	44	12	6 (50%)	2	1 (50%)	17	8 (47%)
Ficus sycamorus	81	>100	10	1 (10%)	0		0	
Commiphora madagascariensis	18	52	8	5 (62%)	1	0 (0%)	4	0 (0%)
Dalbergia melanoxylon	21	60	8	2 (25%)	11	1 (9%)	86	1 (1%)
Acacia sieberiana	39	76	7	2 (29%)	0		1	0 (0%)
Bobgunnia madagascariensis	32	75	6	2 (33%)	3	2 (67%)	16	0 (0%)
Cassia afrofistula	32	40	5	3 (60%)	1	0 (0%)	16	1 (6%)
Albizia versicolor	36	67	4	0 (0%)	0		0	
Antidesma venosum	51	68	4	4 (100%)	0		0	
Combretum kirkii	96	>100	4	0 (0%)	2	0 (0%)	0	
Pericopsis angolensis	24	50	4	1 (25%)	2	0 (0%)	3	1 33%)
Garcinia livingstonei	39	57	3	2 (67%)	0		0	
Acacia nilotica	27	39	2	1 (50%)	1	0 (0%)	6	0 (0%)
Burkea africana	30	38	2	1 (50%)	0		7	1 (14%)
Deinbollia borbonica	33	39	2	1 (50%)	0		1	0 (0%)
Diospyros mespiliformis	56	70	2	0 (0%)	0		0	
Terminalia mollis	76	76	2	1 (50%)	0		0	
Adenium multiflorum	36	36	1	0 (0%)	0		0	
Boscia salicifolia	39	39	1	1 (100%)	0		0	
Cleistochlamys kirkii	49	49	1	1 (100%)	0		1	1 (100%)
Diospyros trucantifolia	65	65	1	0 (0%)	1	1 (100%)	0	
Ehretia amoena	53	53	1	0 (0%)	0		0	
Ochna pulchra	28	28	1	1 (100%)	0		0	
Phyllanthus reticulatus	54	54	1	0 (0%)	0		0	
Schrebera tricoclada	47	47	1	1 (100%)	0		0	
Diplorrynchus condylocarpon							1	0 (0%)
Olax dissitiflora							1	0 (0%)
Thespesia garckeana							1	0 (0%)

* Each cut tree is a single, unique individual. However, because baobabs † and other large species such as *Sterculia* spp. rarely get cut down, it is possible to record bees at the same location from year to year. Therefore, some larger trees with bees which were not cut down were re-recorded in the same location, with an active bee colony from year to year (maximum of one record per year).

How do honeyguides influence miombo tree ecology?

In the second section of this chapter, I hypothesize that honeyguides indirectly influence miombo tree ecology via their behaviour of guiding humans to bees – i.e., that honeyguides take honey-hunters to trees of different sizes and of different tree species compared to those which honey-hunters find without the cooperation of honeyguides. A total of 60 tree species were found with *Apis* bees' nests, and of these 42 (76%) species were found with the cooperation of honeyguides. Of the 48 species found using honeyguides, 98 % of species were recorded with bees' nests more than ten times (Table 5.3).

Whether or not a bees' nest tree was found with the help of a honeyguide had a significant positive effect on the likelihood of the tree being cut down (Estimate = 0.75, SE = 0.09, Z = 8.32, $p < 0.001$) (Figure 5.6B; see also Chapter 2). The inclusion of an interaction term between tree DBH and whether or not the tree was found with a honeyguide's help significantly improved this logistic regression (model 5, Table 5.2) ($\chi^2 = 4.95$, df = 1, $p = 0.02$), indicating that the effect of tree size on the likelihood of a tree being cut is influenced by whether the tree was found with a honeyguide or not (Figure 5.6).

Honey-hunters cut down *Apis mellifera* bees' nests in trees which were overall slightly yet significantly smaller in stem diameter (39.6 ± 0.57 cm DBH, mean ± SE) than trees found without honeyguides (41.8 ± 0.67 cm DBH, mean ± SE) (Figure 5.6C; Wilcoxon rank sum test results: $Z = 4.86$, $p = 0.015$, $n_1 = 552$, $n_2 = 489$). Honeyguides also guided honey-hunters to significantly more trees with bees' nests which were > 2 m off the ground, compared to bees' nests found without honeyguides ($X^2 = 117.5$, df = 1, $p < 0.001$, $n_1 = 2{,}197$, $n_2 = 2{,}861$). The size difference is unlikely to be ecologically important at the landscape level, but indicates that honeyguides are guiding humans to a different subset of trees than those found without honeyguide cooperation.

When the diversity of tree species found with honeyguides was compared to that found without honeyguides, the Simpson diversity index value (which measures the probability that two individuals randomly selected from a sample will belong to different species; Magurran 2013) was 0.975 for trees found with honeyguides, compared to 0.981 for trees found without honeyguides. The similarity in these values indicates highly similar species between the groups. The evenness value (which describes the distribution of individuals across different species) was 0.238 for trees found with honeyguides, compared to 0.239 for trees found without honeyguides. The Shannon-Wiener index value (which combines species richness and evenness) was 3.786 for tree species found with honeyguides, compared to 4.013 for trees found without honeyguides. This indicates that while there may be a similar number of species present in both groups, species diversity is slightly greater amongst the trees found without honeyguides.

The second way in which honeyguides may indirectly influence the trees which are cut down relates to that fact that honeyguides fly. I hypothesized that honeyguides may more easily locate higher-situated bees' nest than humans, and this predicts that honeyguide-found bees' nests should generally be higher in trees. I tested whether bees' nests were more often found higher up in trees (with entrances 2 m off the ground or greater) when located with the cooperation of honeyguides compared those found without the cooperation of honeyguides. I found this to be the case, with significantly more bees nests at 2 m above the ground or greater when found with a honeyguide, compared to those found without a honeyguide's cooperation ($X^2 = 117.5$, df = 1, $p < 0.001$, $n_1 = 2{,}197$ bee trees not guided to, $n_2 = 2{,}861$ bee trees guided to).

Is tree cutting for honey harvests sustainable?

If tree cutting due to honey harvesting is sustainable, then tree resources should not become limited over time, and nor should honey-hunters shift over time from cutting down more preferred species to less preferred species or size classes. I tested this by investigating tree cutting trends from 2017 to 2022. I found that overall, for the fourteen major bee tree species (Figure 5.7), there were no significant changes in cutting rates from 2017 to 2022 (Linear mixed model; estimate = 1.68, SE = 1.89, t = 0.88, p = 0.38). However, when testing species individually in the same model by including an interaction term between year and species, cutting rates significantly decreased for *Combretum adenogonium* (Figure 5.7; Linear mixed model species ~ year interaction term; estimate = -7.04, SE = 2.67, t = -2.63, p = 0.011) and significantly increased for *Terminalia stenostachya* (Linear mixed model species with year as an interaction term; estimate = 6.05, SE = 2.67, t = 2.26, p = 0.02) from 2017 to 2022.

If honey-hunters have shifted over time from cutting down more preferred species to less preferred species or size classes, then we should, first, see a change in the sizes classes of tree relative to distance to the village, due to depletion of preferred intermediate stems in the high-impact zones closer to the village. However, I did not find a significant relationship between cut tree size (DBH) and distance to the village (F = 1.719, df = 1, 841, p = 0.19). Second, if honey-hunters cut down certain species at disproportionately high rates relative to their background stem densities, then tree cutting on these species might be unsustainable, and could be altering the species composition of the landscape. For the major harvested species, I also qualitatively compared the shape (but not magnitude) of background stem densities in relation to size to the harvested stem densities in relation to size (Figure 5.4). These curves reveal that for none of these species are younger trees size classes felled for honey (Figure 5.4). For two species, *Albizia amara* and *Brachystegia spiciformis,* the shape of the relative abundance curves show there is not much recruitment and they have very low densities of small stems (Figure 5.4). This might be due to cohort recruitment or that the juveniles are recruiting in a different part of the landscape from where the adults are found, but it means that there is not an abundant number of juvenile trees to replace those cut for honey.

Next, using a demographic model, I assessed whether rates of recruitment into the size class of trees big enough to host bee colonies were equal to or greater than rates of loss due to cutting. Simulated demographic models for four important bee tree species did not predict – either at current harvesting rates or at rates 10 times greater than present – a notable decline in large 'bee trees' or 'elders' over the next 100 years (Figure 5.9). Under current cutting rates, with 1000 simulations run and 95 percentile parameters plotted, for none of the four species (*Julbernardia globiflora, Terminalia stenostachya, Pterocarpus angolensis* and *Combretum adenogonium*) did stem estimates trend towards zero (Figure 5.9). Modelled stem densities for the larger 'bee tree' and 'elder' classes all increased from the starting point and then stabilized, yet with more variability for *Julbernardia globiflora* and *Pterocarpus angolensis* than for *Terminalia stenostachya* and *Combretum adenogonium*, which were far more stable.

Under scenarios of increased cutting pressure, especially at 10 and 100 times current cutting rates, bee tree and elders (but not sapling) populations did crash in some simulations for *Julbernardia globiflora* and *Pterocarpus angolensis* (Figure 5.9). Differences between the size classes of the predicted stem densities appears similar to the proportions seen between realistic, currently observed size class densities (Table 5.2), supporting the general realism of the demographic model. Importantly, with cutting rates due to honey-hunting 100 times greater than present (true cutting rates are 2–3 times higher than those reported by our subset of honey-hunters from Mbamba village; see Methods), the projected populations may go through demographic bottlenecks due to a reduction in bee tree and elders, but a healthy proportion of saplings persists (Figure 5.9).

Table 5.4. Relative abundance for 50 tree species. These indices are the ranked relative percentage of stems which (1) contain bees or (2) which were cut down, compared to (3) the background abundance of stems (> 10 cm DBH) measured in the vegetation sampling plots. For example, *Terminalia stenostachya* is the most common species in the community (15.2% of the tree plot stems) but is less likely to be found with bees than other rarer species (e.g., *Albizia amara*). However, it is often cut down (second only to *Julbernardia*). Missing data in the vegetation sampling plots indicate insufficient sampling effort to fully represent community structure, often because of their localized habitat preferences (e.g., *Kigelia africana*, *Ficus bussei*).

Species	**Relative abundance of bee trees (% of all bee trees recorded)**	**Relative abundance of trees cut down (% of all cut down trees)**	**Background abundance measured in the vegetation plots (% stems > 10 cm DBH)**
Millettia stuhlmannii	10.5	2.8	9.0
Albizia amara	9.5	6.9	2.0
Acacia nigrescens	8.8	2.7	0.4
Julbernardia globiflora	8.6	17.2	8.2
Terminalia stenostachya	6.0	11.3	15.2
Combretum adenogonium	5.8	6.5	5.4
Erythrophleum africanum	4.6	2.1	1.7
Combretum collinum	3.9	6.9	3.7
Tamarindus indica	3.9	1.9	0.6
Sclerocarya birrea	3.4	4.3	1.7
Pterocarpus angolensis	2.7	3.9	2.1
Acacia rovumae	2.6	0.6	0.4
Dalbergia melanoxylon	2.2	0.3	-
Brachystegia boehmi	2.1	4.1	2.4
Terminalia sambesiaca	2.0	3.4	3.0
Xeroderris stuhlmannii	2.0	2.3	1.0
Syzygium ovariense	2.0	2.1	-
Afzelia quanzensis	2.0	0.4	-
Pseudolachnostylis maprouneifolia	1.9	4.3	4.2
Diospyros kirkii	1.6	1.5	4.4
Ficus bussei	1.4	0.1	-
Berchemia discolor	1.1	0.2	0.3
Brachystegia spiciformis	0.9	1.8	2.3
Sterculia appendiculata	0.9	0.5	-
Lannea schweinfurthii	0.8	1.5	1.0
Kigelia africana	0.8	1.1	-
Philenoptera bussei	0.7	1.2	2.7
Strychnos madagascariensis	0.7	1.1	-
Terminalia sericea	0.6	1.0	-
Syzigium guinensis	0.6	0.9	-
Bobgunnia madagascariensis	0.5	0.3	-
Cassia afrofistula	0.5	0.3	0.9
Sterculia quinqueloba	0.4	0.3	0.1
Sterculia africana	0.4	0.2	-
Piliostigma thonningii	0.4	0.9	-

Schinziophyton rautanenii	0.3	0.2	-
Xylia torreana	0.3	0.4	-
Markhamia obtusifolia	0.3	0.8	0.9
Commiphora madagascariensis	0.3	0.4	3.2
Ficus sycamorus	0.2	0.1	-
Acacia nilotica	0.2	0.1	0.1
Burkea africana	0.2	0.2	1.0
Pericopsis angolensis	0.2	0.2	-
Acacia sieberiana	0.2	0.2	-
Combretum kirkii	0.1	-	-
Albizia versicolor	0.1	-	-
Antidesma venosum	0.1	0.3	-
Deinbollia borbonica	0.1	0.1	2.0
Garcinia livingstonei	0.1	0.2	0.3
Cleistochlamys kirkii	0.0	0.2	2.7

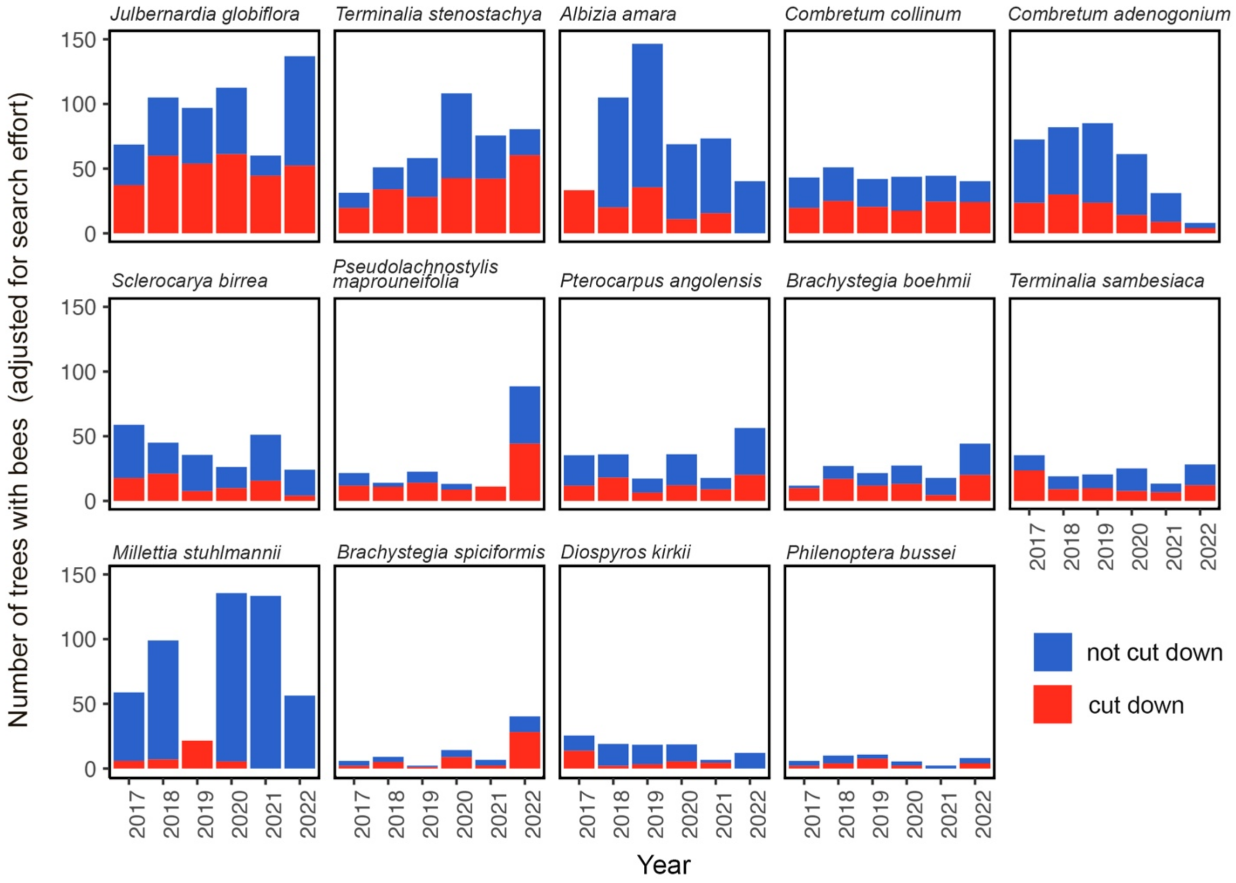


Figure 5.7. Number of trees with bees' nests (*Apis*, *Melipona* and *Hypotrigona*) found from 2017–2022, showing the subsets cut down for honey harvests (red bars), for the fourteen most commonly harvested trees. All values other than for 2019 were adjusted for varying search effort (measured as number of honey-hunter days spent foraging per year). Adjusted counts of bee trees were calculated by multiplying yearly counts by the relative difference between the number of honey-hunter days in the busiest year (447 days in 2019) and those of other years.

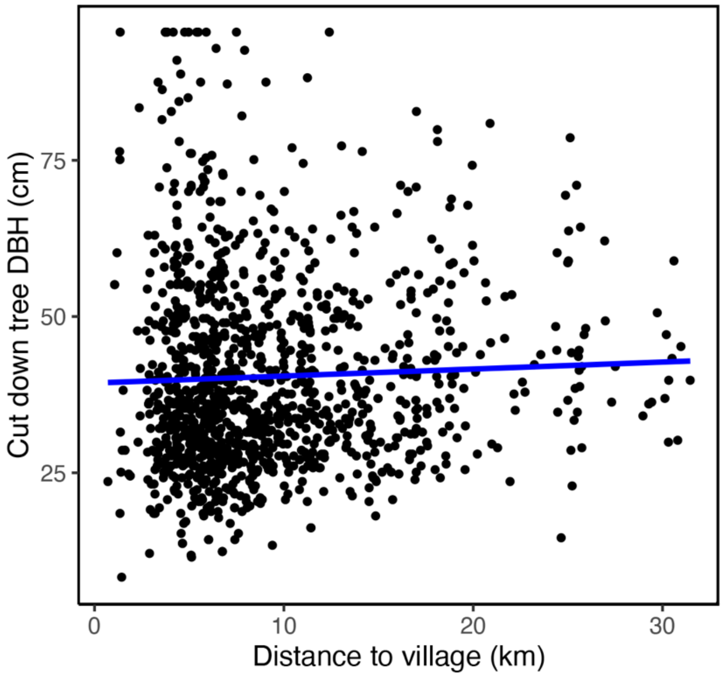


Figure 5.8. Relationship between and distance to village and size of cut down trees (DBH) between 2017 and 2022. Each dot represents an individual tree, and the fitted regression line (blue) shows a non-significant relationship.

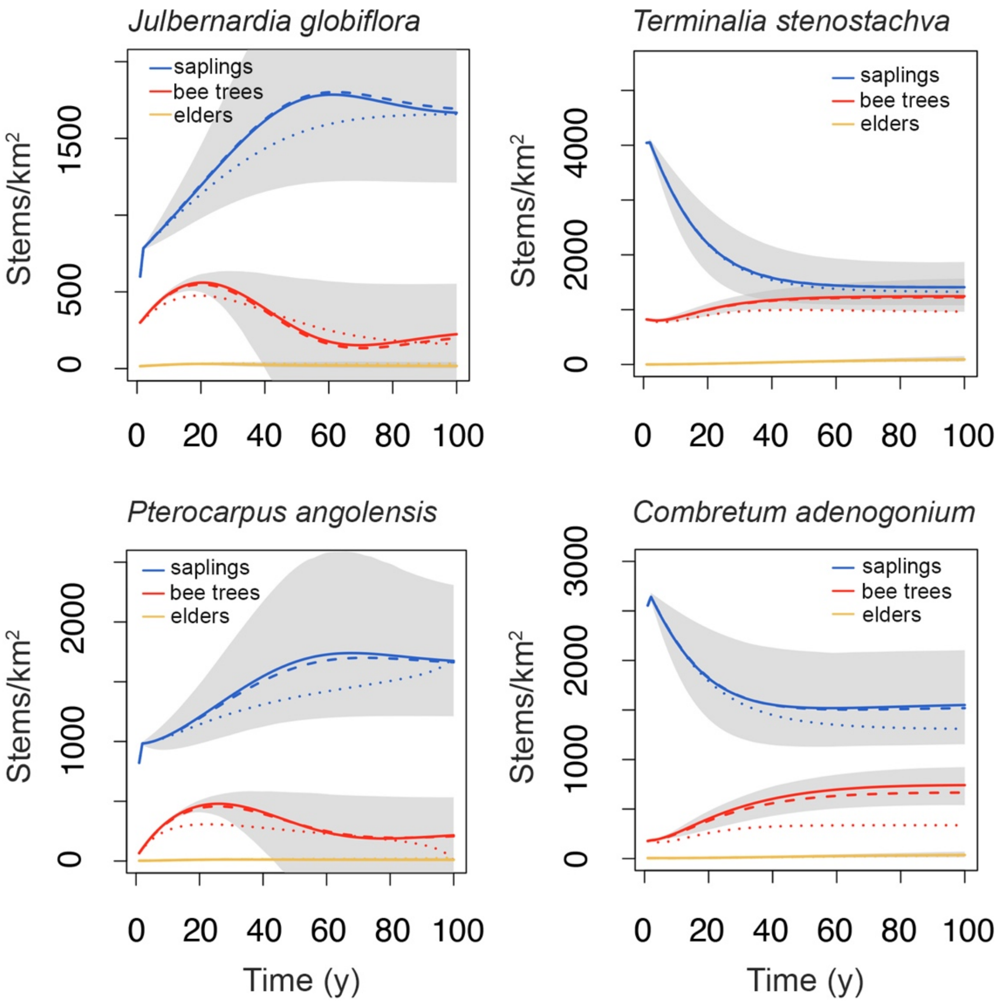


Figure 5.9. Simulated mean change in stem densities (per km^2) for four trees species most cut down by honey-hunters for honey. The solid lines represent mean stem densities from 1,000 simulations at current harvesting rates for three size classes (saplings, bee trees and elders – large trees which are beyond the size at which Yao honey-hunters choose to cut them down for honey). Shaded grey areas represent 95 percent confidence intervals from 1,000 simulations with current cutting rates. Dashed lines represent mean values from 1,000 simulations with cutting rates 10 times greater than currently, and dotted lines for 100 times the current cutting rates. Starting stem densities were set from observed densities for these tree species within in sampling plots. See Table 5.1 for detailed model parameters.

Discussion

The impact of honey-hunting and tree cutting on miombo woodlands

Tree cutting to harvest honey is central to the human-honeyguide mutualism as a means of gaining the sweet payoffs from cooperation. Without the cutting of trees, honeyguides and honey-hunters would both fail much of the time to gain access to the benefits of the mutualism. It is hard or nearly impossible in many cases for honey-hunters to climb the tree and harvest honey without felling the stem. In this chapter I described the impact of honey-hunting on trees around Mbamba village in northern Mozambique from 2017–2022, and explored the specific influence of honeyguides on tree-cutting outcomes. I then attempted to determine whether current tree cutting rates can be considered sustainable, and to do so leveraged one of the strengths of this study system – the ability of honey-hunters to self-collect ecological data in a continuous way over a prolonged period.

From a spatial perspective, the findings in this chapter show a fluctuating level of human activity across the landscape, varying in both time and space (Chapter 2). Tree cutting activity had a strong negative relationship with distance from Mbamba village (Figure 5.2). Bees, as a resource, did not appear to decline between 2017 and 2022 (Figure 5.7), and tree cutting over this period remained most concentrated between 4 and 7 km from the village, particularly near the Lugenda river (Figure 5.2B). This is likely driven by the multiple uses which these riverine habitats offer honey-hunters who also often depend on fishing for their livelihoods. Riverine habitat has also been increasingly cleared for shifting agriculture since 2020. Riverine tree communities along the Lugenda river also appeared to support the highest (or fastest recovering) densities of bees in the landscape (unpubl. data), most likely because of perennial access to water. Therefore, the combined effects of accessibility from the village, access to water, and high bee densities all likely contribute to honey-hunter decisions to use (and revisit) these areas.

I found that after Yao honey-hunters locate a tree with bees, three factors tend to influence their decision of whether to cut the tree down or not. The data show that tree species and tree size are critical (Figure 5.5A). Second, Yao honey-hunters report (pers. comm.) that the quantity of dark propolis markings around the bee colony entrance (for *Apis* bees' nests) is used as an indication of how long the colony has been in the tree for, and so how much honey it is likely to have stored, and therefore be more worthwhile to harvest. Finally, wood hardness is important: tree species such as *Combretum collinum, Terminalia stenostachya, Syzygium* *owariense, Acacia nigrescens* and *Acacia rovumae* (Table 5.3) are known for their hard wood and were rarely cut down once they exceeded 35 cm DBH. For example, of the 258 recorded *Acacia nigrescens* with bees' nests, only 24 (9%) were cut down for honey (Figure 5.5). Conversely three large-growing species, *Sclerocarya birrea*, *Albiza amara* and *Milletia sthulmannii*, were regularly cut down when found with bees' nests, because even for specimens with large diameters the wood is known to be slightly easier to cut into with an axe, and these species often have hollow stems (pers. obs.).

Susceptibility in the tree stems to rot and damage from termites affects a considerable number of trees in this habitat. For example, in the sampled vegetation plots, 14 % of standing *Albizia amara* stems and 27 % of *Pterocarpus angolensis* stems were broken off or hollow, or had damage from elephants, fire or termites. Overall, the wide range of tree species (Table 5.3) and tree sizes in which bees' nests were harvested from (ranging from 12 to 95 cm DBH) show that honey-hunters will at least sometimes cut down large trees when they are hollow and/or they believe them to contain a large honey yield. I found that (apart from the few high wood density species mentioned above), honey-hunter preference generally reflected the species available with bees in the environment (Figure 5.5, Table 5.3). This indicates that it is selection of trees by bees, rather than by honey-hunters, which plays the larger role in determining cutting impact on the ecosystem.

How do honeyguides influence miombo ecology?

The second question addressed is whether via their mutualism with humans, honeyguides have the potential to indirectly influence tree ecology. If this is so, then honeyguides should enable honey-hunters to find a different subset of trees with bees compared to those which honey-hunters find without honeyguides. I previously showed that honeyguides allow humans to find more bees' nests per unit time (Chapter 2), which may simply lead to more trees being cut. Alternatively, however, this may lead to honey-hunters being more selective in which trees they cut down. In this chapter, I show that honey-hunters were more likely to cut down trees shown to them by a honeyguide than trees of an equivalent size which they found without the help of honeyguide (Figure 5.6B). Honey-hunters were more likely to cut down almost any size of tree if they had been guided to it (Figure 5.6B), ruling out the hypothesis that honeyguides allow honey-hunters to be more selective. However, of the trees that were cut down, those that had been found with the cooperation of a honeyguide were on average slightly smaller than those which humans had found alone (Figure 5.6C). This might be because the honey-hunters were more confident of finding large honey rewards in small trees that a honeyguide had guided them to.

Intriguingly, honeyguides also guided honey-hunters to significantly more bees' nests which were > 2 m off the ground, compared to bees' nests found without honeyguides. This is consistent with the idea that honeyguides, being arboreal, have different abilities to detect bees' nests which are high in trees compared to terrestrial humans. Alternatively, humans may have some inherent visual search bias towards spotting bees lower down in larger trees, such as those with many obvious cavities. Taken together, these results suggest that increased rates of cutting enabled by honeyguide cooperation may be offset by the tendency of honeyguides to guide humans to slightly smaller trees (which humans are more likely to then harvest), as well as by the overall very low densities of cutting across the landscape.

Are current tree cutting rates for honey harvests sustainable?

To explore the sustainability of cutting, I investigated rates of tree cutting relative to tree availability, trends in the overall rates of tree cutting over time, and trends in tree cutting (with respect to species and size classes) over time and relative to distance to the village. Specifically, I tested the hypothesis that if honey-harvesting is occurring at unsustainable levels, then honey-hunters should have shifted from cutting down more preferred species to less preferred species or size classes over time, and that we should observe a highly disproportional impact on some species. I also ran demographic simulations for four species commonly cut down to assess whether estimated cutting rates trend towards extinction. Overall, I found minimal evidence that honey-hunting activities are cutting trees down at rates exceeding natural regenerative capabilities.

First, I found that true rates of cutting (number of stems per square kilometer per year) were very low relative to stem availability (Table 5.3). This supports a conclusion that current tree cutting rates, when considered in isolation from other disturbances such as fire or elephant damage, are likely to be sustainable simply because the overall impact is minimal. For example, *Julbernardia globiflora* and *Terminalia stenostachya*, two of the most commonly harvested trees, were cut at rates of 0.09 trees/year/km^2 and 0.08 trees/year/km^2 across the whole area visited by honey-hunters, in comparison with their recorded densities of 1,898 and 4,668 trees/km^2 respectively from the plot data. The overall rate of tree cutting around Mbamba village was 0.6 trees/km^2/year, which is similar to that found for all tree species around Lisongole (0.79 trees/km^2/year), another village in Niassa with a honey-hunting and apicultural community (Riberio et al. 2019). In the North-Western Province of Zambia, where the number of trees debarked for beehives was 3.1 trees/year/km^2 from an available resource of about 224 trees/km^2, Clauss (1992) concluded that ringbarking rates for apiculture was sustainable, suggesting that the much lower rates observed in my study should be sustainable too.

However, tree cutting needs also to be considered with reference to other agents of top-kill (Holdo, 2006). Elephant-related top-kill in miombo woodlands in Niassa is estimated to impact 0.21 % of stems annually, with 0.75 % being top-killed by fire, and 2.04 % due to wind and senescence (Ribero et al. 2008). These rates are much higher than top-kill rates from honey-hunting in the present study, suggesting that honey-hunting is a modest contributor to overall rates of top-kill at Niassa. Accordingly, when current cutting rates (and 10- and 100- fold current rates) were demographically modelled (including estimates of these other ecological drivers of tree demographics), there were no long-term declines projected for four species (Figure 4.9), suggesting that there is currently a balance between tree cutting and natural regeneration rates.

There was also no evidence for a sustained increase in cutting rates, except for *Terminalia stenostachya* (one of the most abundant species in this landscape) (Figure 4.6). This trend is unlikely to be driven by unavailability of cavities in other tree species for bees, as bees' nests continued to be found (but not harvested) across all tree species. More likely, this trend could have been driven by the increasing use by honey-hunters of *Terminalia*-dense parts of the landscape over time. When cutting preferences were compared to bee preferences (Table 5.3, Figure 5.4B), the most at-risk species were those which form a relatively small proportion of the total number of stems, but which bees readily move into and which honey-hunters favour cutting down. Two such species worth monitoring for a tree-cutting driven decline would be *Brachystegia boehmii* and *Pseudolachnostylis maprouneifolia* (Table 5.4, Figure 5.5). Moreover, the tree plot data show that both *Albizia almara* and *Brachystegia spiciformis* lack saplings in this landscape (Figure 5.4), while the adult trees are still cut at similar rates to what is available, which suggests that further monitoring might be desirable for these species too.

The interaction between bees' nest tree selection and cutting practices raises the question of whether the cutting of trees with bees can ecologically self-regulate. For example, if areas of the landscape with bee trees are over-utilized by humans, then bee colonies or optimal cavities for bee occupancy are likely to reduce in density (Deitmann et al. 2009, Visick and Ratnieks 2023), making these areas suboptimal for honey-hunters and forcing them to move elsewhere for a period of time. Yao honey-hunters report that parts of the landscape which 'produce good amounts of honey' vary from season to season and year to year, leading them to change where they choose to go honey-hunting (Chapter 2). This could spread the impact of cutting across larger areas, reducing localized cutting pressure while also providing periods of tree cutting relief. Because trees with bees form such a small subset of the total tree community, it is highly likely that bee populations would collapse from overharvesting long before the tree population could (Deitmann et al. 2009, Visick and Ratnieks 2023).

Disturbances in miombo woodlands other than tree cutting for honey, such as fire and herbivory by elephants, are also important factors shaping miombo ecosystem structure and composition (Ribero et al. 2008) and have been found to alter tree densities in parts of Niassa (Ribero et al. 2013). Elephants damage trees in many ways, including uprooting and and de-branching large trees which can open canopy gaps, and in turn promote increase grass growth, which in turn feeds dry-season fires (Beuchner and Dawkins 1961). Fires, and in particular 'hot' late dry-season fires, can burn across large areas and impact vegetation by top-killing gullivers and sapling-sized trees (Archibald 2016). Fire also provides another way in which honey-hunters can have wide-reaching impacts on a landscape, since the fires lit by honey-hunters sometimes go out of control and may have specific seasonality (Tinley 1977). Fires lit by honey-hunters for subduing bees may therefore have much wider-reaching ecological impacts than tree cutting (Tinley 1977; Cuthill 2024) and are not accounted for in this study. It is also possible that the honey-hunters have altered the species composition of this woodland over evolutionary time, and that the currently observed tree community reflects this.

Tree cutting for honey is less densely concentrated around human settlements compared to other forms of human impact on savannah woodlands, such as the cutting of trees for shifting agriculture, cutting for fuelwood (Twine and Holdo 2016), cutting of trees for building materials and ringbarking of trees to construct beehives (Ribero et al. 2019), although more concentrated than the potentially wide-reaching influence of fire. This means that areas of tree cutting damage overlap widely with miombo and riverine woodlands shaped by fires and herbivory. Future work therefore needs to integrate the impact of honey-hunter fires along with impacts of tree cutting activity, to form a more complete picture of how honey-hunting activity affects the ecosystem.

Conclusions

The findings in this chapter help us better understand the impact of a bird-human mutualism on woody savannahs. Unlike tree cutting for fuelwood (e.g., Twine and Holdo 2016), honey-hunters cut a wide range of tree sizes, some of which coppice and recover, and since honey-hunters in the study area never used use saws to cut down trees, they were limited by what they could cut using an axe. Despite concerns over this practice from policy makers (Ribeiro et. al. 2019), several lines of evidence indicate that the cutting down of trees due to honey-hunting in the landscape around Mbamba village, Niassa, is not affecting stem densities or size class distributions at present rates. We do highlight a few species that, due to their high likelihood of being found with bees and being cut when found with bees, and their low background rates in the landscape and/or evidence of low recruitment rates, would be important to monitor in future. The overall impact of tree cutting across the landscape was minimal, honey-hunters did not excessively cut down low-density species, most trees cut down were of an intermediate size, and the number and species of trees cut down for honey did not change for all but two species between 2017 and 2022. Tree cutting also did not lead to a decline of trees big enough to host bees in simulated demographic models for four species commonly cut down. Future work on the impacts of tree cutting should be integrated into the effects of fires lit by honey-hunters on the ecosystem, as well as the feedback between bee density, fire intervals and past tree cutting trends. The engagement of the local community, who possess a deep traditional ecological knowledge of these miombo woodlands, has helped reveal how honey-hunting occurs at low densities over large geographical areas.

CHAPTER 6

Synthesis

Preamble

In this chapter, I revisit the thesis rationale in light of the empirical work in chapters 2 to 5. I synthesise the results from all data chapters under three themes: 1) why cooperate, 2) how local ecology influences the mutualism, and 3) how the mutualism impacts local ecology. I then discuss future research directions and points of interest that emerged from the thesis but are not addressed elsewhere.

In this thesis I aimed to better understand cooperative behaviours and decision-making in the honeyguide-human mutualism, and how the mutualism is shaped by, and shapes, its local ecological context. Specifically, I sought to gain insights into the benefits of participating in the mutualism relative to non-participation using a 'cost-benefit' lens, and to measure whether asymmetry in the rewards gained (where one partner benefits more from cooperation) could lead to mutualistic breakdown. Next, I studied the ecological context of honeyguides as wax-eaters, and the fate of this unusual, energy-rich food in the Niassa landscape. Third, I aimed to measure the costs of cooperation and consequences of non-cooperation (i.e., could non-rewarding behaviour by humans lead to unusual behaviour such as guiding to non-bee animals). Lastly, I sought insights into whether the human-honeyguide mutualism modifies the impact of honey-harvesting on the landscape, and therefore the sustainability, of honey-harvesting in a savannah woodland landscape.

Why cooperate?

This is the core question within the human-honeyguide (and many other) mutualisms. In this thesis, I show that cooperation with honeyguides benefited humans by reducing their search time for bees and increasing honey yield. Reciprocally, cooperation benefits honeyguides by providing access to beeswax which would not otherwise be available. These finding align with prior work undertaken in Kenya (Isack, 1987) and Tanzania (Wood et al. 2014) showing that cooperation with honeyguides increases the rate at which humans find bees' nests. The data-collection system implemented for this research, with Yao honey-hunters from Mbamba village acting as both participants in and observers of the mutualism, allowed for the possibility of also determining whether honeyguides guide humans to trees with more honey overall. From over a thousand honey harvests, I did not find that Yao honey-hunters consistently gained more honey from a bees' nest found by following a honeyguide, compared to a bees' nest found without a honeyguide's assistance. I did, however, find that honey-hunters were more likely to harvest a bees' nest found with the cooperation of a honeyguide, possibly because honeyguides tended to guide humans to slightly smaller trees containing bees' nests (Chapter 5). On days when honey-hunters had more interactions with honeyguides, honey-hunters were more likely to gain a larger cumulative quantity of honey for that day (Chapter 2; Figure 2.9). Taking a day-length perspective of the benefits of cooperation is a novel approach to this question.

How do honeyguides benefit from these interactions? I found that despite the cultural norms of leaving a wax reward for honeyguides at a bees' nests they were guided to, Yao honey-hunters did not leave significantly more wax when they were guided to a tree compared to when they were not guided there. The amount of wax (usually with brood comb mixed in) left behind for honeyguides was best predicted by size of the tree it was harvested from. In Chapters 2 and 3, I concluded that honeyguides most likely benefit from almost every harvest, because of the opening of the nest and subduing of the bees rather than the quantity of wax actively left behind by honey-hunters. Specifically, smoke used by the honey-hunters to reduce bee aggression makes it safer for the honeyguide to approach the bee tree and scavenge pieces of wax, and the opening of small entrance holes using an axe makes physical access for the honeyguide possible in situations that were not previously possible. These factors allow honeyguides to feed on biologically relevant quantities of wax (for a ca. 50 g bird) even from small fragments of wax lying on the ground after a harvest or gleaned by entering the harvested tree trunk (Chapter 3).

Data contained in this thesis also allowed for human-honeyguide interactions to be characterized at a spatial level not previously undertaken to the same degree. I found that over an area of 812 square kilometres, from 2017 to 2022, honeyguides were recorded by honey-hunters in every part of the landscape containing wild bees' nests. Interactions with honeyguides increased away from Mbamba village beyond 7 km, but remained more or less consistent up to 25 km from the village, beyond which honey-hunters rarely walked (except if travelling somewhere). Honey-hunters gained increased payoffs of finding 'higher quality' bee-trees (i.e., those yielding greater quantities of honey) when moving into further from the village into less-visited foraging patches. I found that some of the most productive landscape areas for honey-hunting, especially along the Lugenda river, were consistently productive for honey-hunter from year to year despite being within a 5 km walking distance for honey-hunters.

The behaviours required for successful cooperation between honeyguides and humans are discussed in depth in Chapter 2. Echoing previous research (summarized in Chapter 1), I found that honeyguides guide humans to bees' nests in a generally straight trajectory, demonstrating that they remember and store spatial information about where bees' nests are located. Over thousands of recorded interactions, humans successfully found bees' nests after being guided by a honeyguide more often than they failed. In Chapter 2, I highlighted (without testing in detail) the importance of consistent vocal signalling between honeyguides and human during interactions. Past work (especially Isack 1987; Spottiswoode et al. 2016; Spottiswoode and Wood 2023) highlights the critical role of sound in soliciting guiding interactions from honeyguides and for signalling willingness to cooperate by humans. Do honeyguides need to learn local signals of cooperation? Evidence thus far suggests that they benefit from doing so (Spottiswoode and Wood 2023), but the mechanisms by which they learn are not well understood.

Puzzles in the use of vocal signals for cooperation

If learning local signals of cooperation (and other associated guiding behaviours such falling silent at a bees' nest) is important for honeyguides, we would predict that young honeyguides should less frequently approach humans and initiate guiding than older honeyguides. Plumage differences make it easy to tell if a honeyguide is younger than ca. 13 months old (see Chapter 1). From 13 to 19 of May 2018 and 11 to 29 of June 2019, along with Claire Spottiswoode, I attempted to experimentally test whether juvenile honeyguides were less likely to respond to signals soliciting cooperation than adults. We conducted 87 transects with speaker playbacks of repeated audio loops of either (1) the locally specialized 'brrr-hmm' call, or (2) control treatments of one of two arbitrary human sounds (either a honey-hunter calling his name, or a honey-hunter calling 'sego, uchi' ["honeyguide, honey"]), closely following methods in Spottiswoode et al. (2016). After 87 playback transects, we unfortunately did not gain enough responses from juveniles to conclude whether juveniles were less likely to respond to local signals of soliciting cooperation compared to adults. We were guided by juveniles only three times and found bees once, all in response to control playbacks.

While the experiment was unable to satisfactorily answer the question it was designed to test, it raised some interesting questions. In this dataset, we found that (mostly adult) honeyguides were only slightly more likely to respond to recordings of local 'brrr-hmm' signals (57% of transects) compared to human control sounds (48% of transects). This is a weaker effect size than found in prior studies (Spottiswoode et al. 2016, Spottiswoode & Wood 2023). One possible reason for this could be that because many of these playbacks took place > 25 km from the village, naïve honeyguides may have been attracted to any sound made by a human, having had less opportunities to learn local signals compared to honeyguides in areas where more frequent honey-hunting occurs (Figure 2.2). A second possible reason could be that because this playback experiment was conducted at the same time of year as peak honey-hunting activity, unlike prior experiments. Therefore, honeyguides may have possibly encountered an altered ratio of honey-hunters relative to other non honey-hunting humans (when compared to prior playback experiments) in a way which alters the value to honeyguides of discriminating between humans.

Experimental work so far has focussed on the types of calls given to *attract* honeyguides, and more work needs to be undertaken to understand whether and how the timing and regularity of calls made to honeyguides *whilst* being guided, as well as their type, influence guiding success. My direct impressions (based on > 205 days of fieldwork and > 300 first-hand experiences of being guided to bees' nests whilst accompanying Yao honey-hunters, and also being guided alone by a honeyguide to a bees' nest in Niassa three times whilst using local signals of cooperation) is that constant vocal signalling by the human to a honeyguide has at least two functions. Constant vocal signalling appear to repeatedly communicate willingness to maintain cooperation, and when visual contact is lost, is used to signal relative position when both parties are moving. Specific human calls, such as the 'brrr-hmm' call, used to *attract* honeyguides are probably more successful overall because they communicate identity ("I am a honey-hunter'). But after the honeyguide arrives at the honey-hunter and cooperation begins, vocal signals from both parties likely do not need to communicate identity so much as their relative position and a willingness to continue cooperation. By constantly calling to a honeyguide when being guided, honeyguides appear to be better able to track a honey-hunters' position as they lead them and also to react by doubling back if they stop following. This two-way 'conversational' aspect of honey-hunting is currently understudied, and I plan to investigate it in more detail using the dataset of audio recordings of both the honeyguide and the human over the duration of honey-hunts, also used for other questions in Chapters 2 and 4.

How local ecology influences the mutualism

In Chapter 3, I found that in Niassa, a surprising number of species other than greater honeyguides eat beeswax. Conspecific and heterospecific competition for the benefits of a resource has been shown to have important implications for mutualisms (Jones et al. 2012), yet the human-honeyguide mutualism, despite the risk posed by third-party competitors, it is not on the verge of mutualistic breakdown (Fredrickson 2017). Rather, in Niassa, inter- and intraspecific competition appears to play a role in stabilizing mutualistic dynamics by conferring the greatest benefits on early-arriving guiding honeyguides, who benefit by gaining the best quality wax ahead of scroungers (see also Cram et al. 2023).

These findings align with other recent work from client-cleaner mutualisms showing that the presence of third-party species alters the cleaning behaviour of brain coral by sharknose gobies *Elacatinus evelynae*, making it more consistent (and therefore possibly more stable) (Dunkley et al. 2022). In another African study system, 'third-party' scale insect species were found to strengthen an ant-plant mutualism by providing mutualistic ants with an alternative source of food when resources from the extra-floral nectaries of their plant mutualists were producing less (such as during annual dry periods). When scale insects were experimentally removed, ant defences reduced and the plants became at greater risk from catastrophic damage from mega-herbivores (Prior et al. 2018). Thus, the way in which wax-eating competitors reinforce rather than jeopardize the human–honeyguide mutualism is similar to how scale insects stabilize ant-plant mutualisms.

How the mutualism influences local ecology

Tree cutting and the lighting of fires in order to access honey and subdue bees using smoke are central components of the human-honeyguide mutualism for both species to gain a food benefit from cooperation. In Niassa, if honey-hunters are restricted from cutting down trees to access honey, the mutualism would fail for the majority of cooperative interactions. From direct observations, in the majority of cases it is harder and more risky for honey-hunters to climb a tree with bees and harvest honey without felling the stem. Also increased are the risks to humans of harvesting bees' nests, which is dangerous even *with* the use of smoke, and can be lethal to do so without. As would be predicted from ecological foraging models, human decision-making seeks to reduce the energetic costs of harvest wherever possible (Koster and Bird 2024), so it is therefore no surprise that Yao honey-hunters make decisions which reduce energy expenditure and risk. In Chapter 5, I described the impact of honey-hunting on trees around Mbamba village in northern Mozambique from 2017–2022, and explored how honeyguides specifically influence this impact. I found that honey-hunters cut down a wide range of tree sizes and species, some of which coppice and recover, and that since honey-hunters were limited by what they could cut using an axe, did not cut down all trees they found containing bees' nests.

Honey-hunters were more likely to cut down any size of tree containing a bees' nests if they had been guided to it by a honeyguide. Yet of the trees that were cut down, those that had been found with the cooperation of a honeyguide had a slightly smaller diameter at breast height than those which honey-hunters found alone. Honeyguides were significantly more likely to guide honey-hunters to bees' nests with entrance holes higher than 2 metres above the ground. This finding supports the idea that honeyguides' capacity for flight affords them different abilities to humans at detecting bees' nests, and specifically that they may be better than terrestrial honey-hunters at locating bees' nests which are high in trees.

Overall, I concluded that in Niassa the impact of tree-cutting for most species was sustainable, primarily because honey-hunters cut down very low numbers of stems (per square kilometre) and do not excessively cut down low-density species. Most trees cut down for honey-harvests were of an intermediate size, and the number and species of trees cut down for honey did not change for all but two species between 2017 and 2022. In simulated demographic models for the four tree species most commonly cut down, current cutting rates did not lead to a decline of trees big enough to host bees. Future work on the impact of tree cutting needs to be integrated into the effects of fires lit by honey-hunters, with careful consideration to the feedback between bee density, fire intervals and past tree cutting trends. My findings on tree cutting impacts from honey-hunting should be interpreted hand-in-hand with those of Cuthill (2024), using the same honey-hunter dataset to show that fire ignitions made by honey-hunters in this landscape only accounted for a small proportion of overall wildfires, yet could either spread widely or be useful from a management perspective by acting as firebreaks to subsequent more destructive fires, depending on when the fires were lit.

In a final note, from time working on this thesis, it is hard to overstate the role of the humble (but not innocent) axe in constraining the impact of honey-hunting on this landscape. The continued use in Niassa of locally-made axes using *Combretum* spp. wooden handles, and locally-forged steel axe-heads shaped from scrap metal (often old vehicle leaf-springs), is perhaps the primary thing standing between honey-hunting sustainability and unsustainability. In Chapter 5, I reported how honey-hunters often comment on the constraints that the strength of their axes place on the harvest of large or hard-wooded tree species. If honey-hunters in Niassa were to start using tools other than axes to cut down bee trees (such as the long, two-person, hand-held, crosscut saws I have observed being transported by motorbike for felling trees in the woodlands of southern Tanzania), the cost-benefit balance and decision making around which stems to harvest would be rapidly altered. In the future, conservation managers will need to balance the needs of local communities, who possess a deep traditional ecological knowledge of miombo woodlands – and a special role in an ancient mutualism – with an awareness of how human behavioural and technological changes could have wide landscape-level repercussions.

The impact of honey harvests on bee colonies

Regrettably, African honeybees (*Apis mellifera scutellata)* and their colonies have not been discussed as much as I would have liked in this thesis. An obvious question about the ecological impact of honey harvesting arises from reading Chapter 5: what happens to the bee colonies after their nest is harvested? How many of them survive? I cannot offer an exact answer to these questions but can offer some clues from what is known about African honeybees in general. It is known that because of a tropical climate, African honeybees generally store less honey and have more variable colony sizes than European honeybee subspecies (*Apis mellifera mellifera*) (Johnson, 2023). They take 18.5 days to complete larval development, which is 2–3 days less than European honeybees, and do not need to store as much food as temperate-climate bees who do so for survival during winter (Schneider and Blyther 1998). With fast growth and often without as large an investment into stored food, African honeybee colonies split more readily, and also more readily abscond from a poor nesting sites, but may also abscond because of parasites or predators (such as honey badgers) or because of wildfire (Schneider and McNally, 1992).

In a temperate climate, harvesting a wild bee colony and taking all its food (honey) almost certainly results in the death of a bee colony (Seeley, 1985). Dietemann et al. (2009) suggests that the same is likely true for African honeybees, but that their survival chances are heavily influenced by the size of the colony, the time of year of harvest (affecting food availability for reestablishment), and by a more forgiving climate. It is therefore likely that after harvests in our study area, some bee colonies survive. If the queen bee survives a harvest, if fire is not used excessively (which causes death by heat to bees) and particularly if the bee tree is not felled, then the chances of survival for the colony likely increase. I have noticed that the harvests of large, exposed bee colonies in baobab trees (108 such colonies in baobabs were recorded by Yao honey-hunters in the area) are typically non-fatal and that bee colonies tended to persist and recover in the same location. On some occasions, even while the honey-hunters were still harvesting honey, the bee colony would gather in a tree or under a branch nearby and then fly off away as a swarm. Overall, however, it is probable that the majority of bee colonies harvested using traditional methods in Niassa eventually die (Dietemann et al. 2009).

What five years of data (and the cooperation of honeyguides freely sharing their knowledge) has shown us is that bee colonies are abundant in the Niassa landscape (we estimate densities of 14.5 colonies per square kilometre in riverine habitat), making it comparable to some of the highest bee colony densities in Africa (Jaffé et al. 2010). The historically reported abundance of bees in Niassa (see Chapter 1) persists, and around Mbamba village we did not detect a decline in bees' nests found by honey-hunters from 2017 to 2022. Wild bees in Niassa, like in most areas of Africa, are likely far more threatened by widespread habitat modification (Dietemann et al. 2009) than from traditional forms of honey-hunting. Therefore, as long as honey-hunters continue covering large areas in search of bees (Chapter 2), do not harvest or cut down all the trees they find with bee colonies (Chapter 5), and that the widespread clearing of miombo habitat with tree sufficient cavities for bee colonies to occupy does not take place, then healthy bee populations in Niassa should persist.

Implementing an icon-driven ecological data collection system

Indigenous human communities and cultures often make valuable (and regularly underappreciated) contributions to towards assimilating traditional ecological knowledge into modern scientific frameworks (Berkes et al. 2000; Liebenberg et al. 2016). The very existence of this thesis is heavily reliant on the detailed behavioural and ecological information shared by Yao honey-hunters living alongside, and cooperating with, honeyguides in Niassa Special Reserve. In 2017, to better collect data on human-honeyguide interactions, we developed an icon-driven software application that was loaded onto ruggedised smartphones. This concept had already been tested in the form of CyberTracker for the purposes of collecting ecological data on endangered and rare animals via the skills of Indigenous trackers in southern Africa (Liebenberg et al. 2016), and a predecessor of our application (in our pilot study at Niassa) used the CyberTracker platform. However, due to the uniqueness of the human-honeyguide mutualism, a more customised platform was necessary to properly accommodate a series of steps which mimicked the natural decision-making points in human-honeyguide interactions. This was implemented with the professional programming and database design assistance of a commercial company; HabitatInfo (Wales, UK).

The customised, icon-driven nature of our application was a necessary step due to the low levels of literacy amongst the Yao honey-hunters we collaborated with. I found that some aspects of initial icon and application designs were difficult for honey-hunters to interpret (e.g., the colour associations between green for a positive interaction versus red for a negative interaction did not carry the same cultural associations, and the open number ‘4’ on the LCD screens of the electronic scales used to weigh honey and wax was not recognised as being the same number as the closed letter ‘4’ as printed here for when honey mass was inputted into the app). Multiple rounds of app design changes (eleven in total, becoming progressively minor), were required to refine both the correct usage and correct interpretation (and memorization of) the icons. Multiple rounds of training days were also undertaken in which I accompanied groups of honey-hunters and observed data input behaviour. Because of the use of smartphone

GPS to collect spatiotemporal data, particular care had to be taken to emphasise that the data needed to be inputted as quickly as possible at each step (i.e., taking the device from a pocket and clicking on the 'Followed honeyguide' as soon as the honeyguide began guiding). Honey-hunters varied in how quickly their input error rates dropped, and those who learnt quickest were instrumental in training other members of the honey-hunter data collection group.

When implementing our data collection system, I found that: i) the data entry error rate stabilised after a short period of time; ii) data-entry errors were highly predictable and possible to detect due to the temporal and spatial details collected by the app, together with the photographs taken; iii) it was possible to reduce errors through both the redesign of the app and detailed training sessions; and (iv) with contextual understanding of what honey-hunting behaviour looks like on the ground it, it was possible to correctly filter data and in some cases correct it using a custom, logical, R application designed in collaboration with Brian Wood. The multifaceted use of audio, GPS and visual recording capabilities made this system powerful. As detailed in Chapter 5, the audio-recording of tree species names was particularly accurate, which, when combined with photographs for verification purposes and spatial coordinates, made for a dataset which would have been impossible for visiting scientists (such as ourselves) to collect. We plan to publish in detail the lessons learned from this data collection system in the near future, hopefully encouraging other scientists to use custom-designed systems which enable the holders of Indigenous ecological knowledge to share it.

Conclusions

This thesis presents and links numerous ideas and observations on cooperative behaviour and the place of the human-honeyguide mutualism within its ecological context. In it I highlight a common thread between the behaviour of a yellow-throated sandgrouse (*Pterocles gutturalis*) backing away from a human threatening its chick, while making a distracting croaking call and keeping track of both the position of the human and its chick relative to itself, and a honeyguide guiding a honey-hunter to bees, whilst flying from tree to tree and producing a chattering call while also keeping track of both its position and that of a honey-hunter relative to its honeybee destination. These behaviours touch on the question of how complex spatial navigation skills evolve, or are acquired and develop. Do birds need to learn how and when to apply such behaviours? Are these behaviours truly innate? If a honeyguide guides someone to a dangerous snake and not a bees' nest, the findings in Chapter 4 should lead to the conclusion that it this likely not punishment for previously not rewarding the bird with sufficient beeswax, but rather, more likely to be a spatial recall error analogous to that of a nuthatch *Sitta* sp. making a spatial error in the retrieval of stored food items.

If a human, armed with nothing but this thesis and no prior knowledge, were attempting to cooperate with a honeyguide in an African savannah woodland containing wild bees' nests, they would have noted both the essential behaviours for cooperation and some of the uncertainties from this study. A guiding honeyguide could be first attracted using acoustic signals (ideally sounds commonly used in that local context) and once a honey-hunt was initiated, the honeyguide would guide relatively directly to a bees' nests – chattering continuously, flying with an obvious dipping flight, and responding readily to frequent vocalisations made by the following human. The timing and rhythm of calls directed at the bird would likely to contribute to the successful outcome of finding a bees' nest, although in ways not yet fully understood.

If such a honey-hunt were taking place in Niassa, and if, after finding a bees' nest (having overcome the challenges of spotting it), a decision was made to harvest it by cutting the tree down, the findings in Chapter 5 would offer some cautious reassurance about the impact of this action on the landscape. The long distances walked per bees' nest and the relative intactness of Niassa's miombo woodlands would support the conclusion that tree-cutting practices, although damaging to individual bee colonies, are likely sustainable at current rates.

Following the honey harvest, cultural practices in Niassa would suggest that a wax reward be left for the guiding bird. If this was done, the findings in Chapters 2 and 3 show that not only the honeyguide will benefit from the beeswax reward. In fact, such intentional wax rewards may not even be necessary for cooperation to persist, because by simply harvesting the bees' nest and providing access, the human half of the mutualistic "contract" is fulfilled. In this way – by calling to and following a honeyguide, finding bees, then rewarding or depriving the bird – a person partakes in a behaviour observed across Africa for millennia, whose repetition across time helps maintain an ancient and remarkable mutualism.

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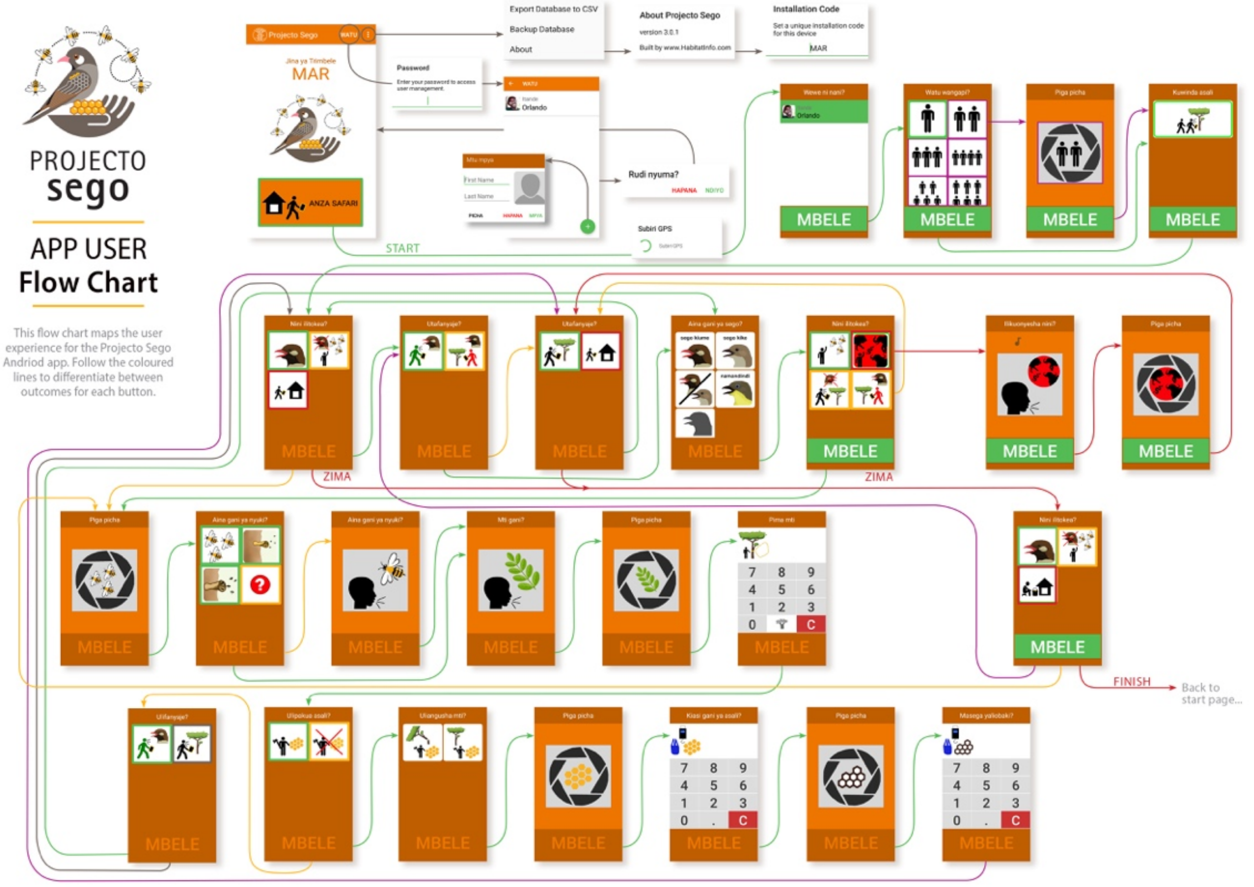
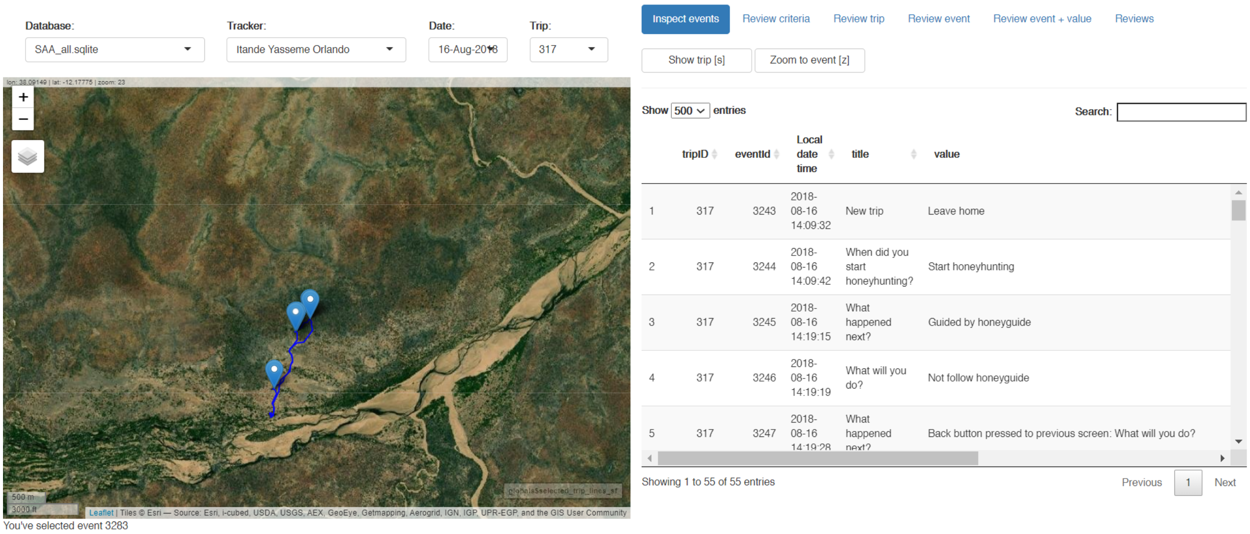
APPENDIX to CHAPTER 2



This flow chart maps the user experience for the Projecto Sego Andriod app. Follow the coloured lines to differentiate between outcomes for each button.

Projecto Sego App *Version 3.1.* Designed by Claire Spottiswoode and David Lloyd-Jones. Developed by Andrew Rayner at Habitat INFO. Flowchart by David Lloyd-Jones, October 2018.

Figure A.1. Diagram of the final version of the custom-developed application loaded on rugged smartphones and used to collect honey-hunting data.



Database: SAA_all.sqlite

Tracker: Itande Yasseme Orlando

Date: 16-Aug-2018

Trip: 317

Show 500 entries

Search:

	tripID	eventId	Local date time	title	value
1	317	3243	2018-08-16 14:09:32	New trip	Leave home
2	317	3244	2018-08-16 14:09:42	When did you start honeyhunting?	Start honeyhunting
3	317	3245	2018-08-16 14:19:15	What happened next?	Guided by honeyguide
4	317	3246	2018-08-16 14:19:19	What will you do?	Not follow honeyguide
5	317	3247	2018-08-16 14:19:28	What happened next?	Back button pressed to previous screen: What will you do?

Showing 1 to 55 of 55 entries

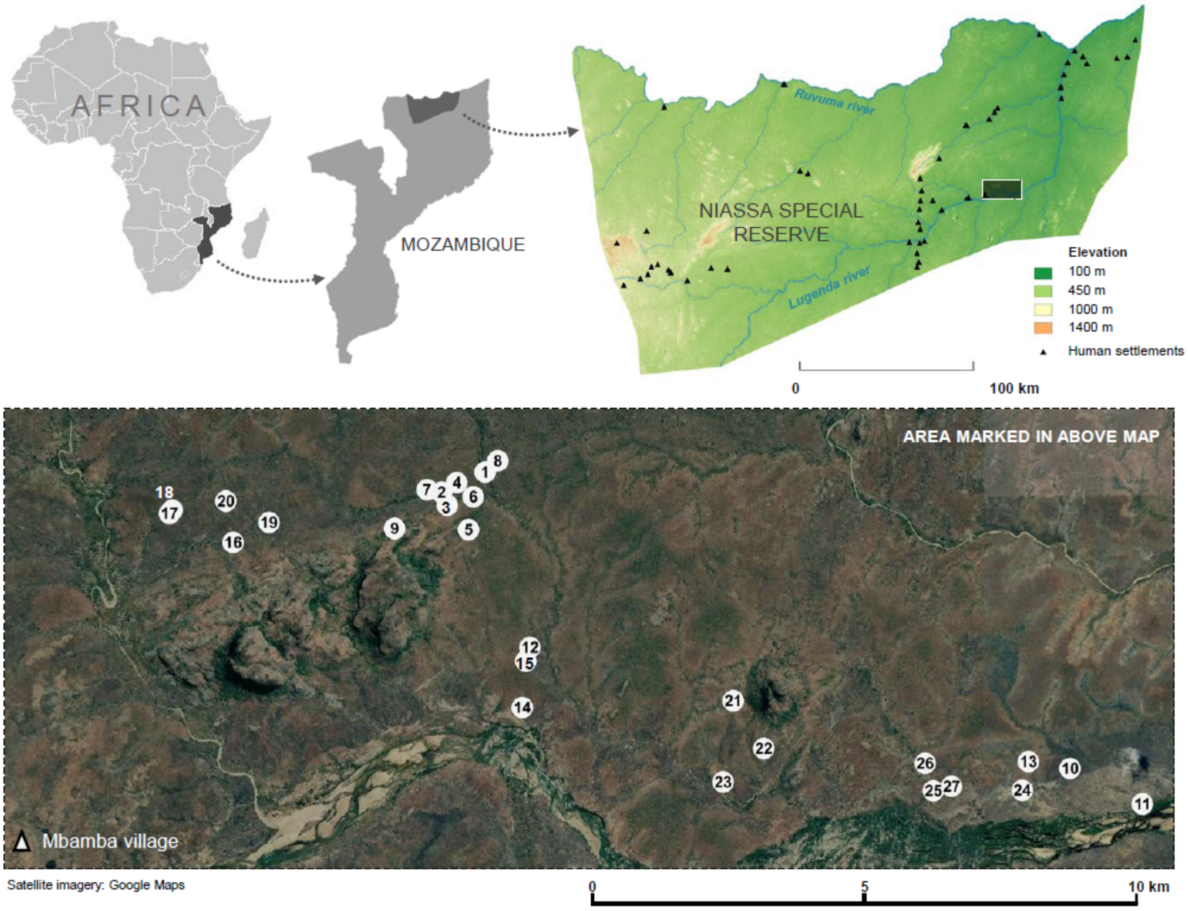
You've selected event 3283

Figure A.2. Screenshot of the graphical user interface of the R Shiny application used to review honey hunting data. On the left the user can scroll around a satellite map with the complete honey hunting trip displayed. Point with images are marked with blue icons.

Table A.1. List of review criteria used to query point ("event") and GPS track data using the trip inspector R Shiny application. These questions were designed so that data could easily be filtered on the basis of a review of 'True', 'False' or 'NA'.

Input value from the application	**Review level**	**Review criteria**
Did you cut the tree down?	event	Was this question (tree cut down) answered correctly?
Did you harvest the honey?	event	Was the honey harvested?
Did you open the bees' nest?	event	Was the honey harvested?
Did you open the bees nest?	event	Was this question (did you open the bees nest) correctly answered?
How much of the honey will you sell?	event	Is the value for how much honey will be sold realistic?
How much wax did you leave behind?	event	Is the value for wax left behind realistic?
Leave home	event	Does this trip originate from a fishing camp or village?
Measure the circumference of the tree	event	Does the tree circumference correspond to the photograph of the tree and is it realistic?
Measure the tree	event	Does the tree circumference correspond to the photograph of the tree and is it realistic?
Leave home	event	Does this trip originate from a fishing camp or village?
Take a photo	event	Does this show a honey-gathering group of people?
Take a photo of the bees nest	event	Does this photo show the location or probable location of a bees nest?
Take a photo of the bees' nest	event	Does this photo show the location or probable location of a bees nest?
Take a photo of the honey	event	Does this photo show honey gathered?
Take a photo of the tree leaves	event	Does this photo show the leaves of the tree reported having bees?
Take a photo of the wax	event	Does this photo show wax left for a honeyguide which corresponds to the value weighed?
Take a photo of what you found	event	Does this photo correspond to the sound recording of the item found?
Weigh the honey	event	Is this value realistic and corresponds to the image of honey left behind?
Weigh the wax	event	Is the value for wax left behind realistic?
What did you do?	event	Does what the honey-hunter did fit within the trajectory of the honey hunt?
What did you find?	event	Does what the honey hunter found correspond to a voice recording of the finding?
Guided by a honeyguide	event	Does what happened next fit within the trajectory of the honey hunt?
What kind of bee?	event	If harvested, does the kind of bee match the honey and wax photos?
What kind of honeyguide?	event	Is this event correctly located in the trajectory of the honey hunt?
What kind of tree?	event	Is this recording made at the same location as the photo of the tree?
Follow the honeyguide	event	Does the action taken fit within the context of the honey hunt?
Start honeyhunting	event	Is the starting point located realistically?
Start Trip	event	Is the starting point located realistically?
Start Trip	trip	Is this an unaccompanied honey hunt (i.e., not a training trip)?

APPENDIX to CHAPTER 3



Satellite imagery: Google Maps

Figure A.3. Location of Niassa Special Reserve in northern Mozambique along with the location of honey-harvest sites where the fate of wax was recorded (n = 26).

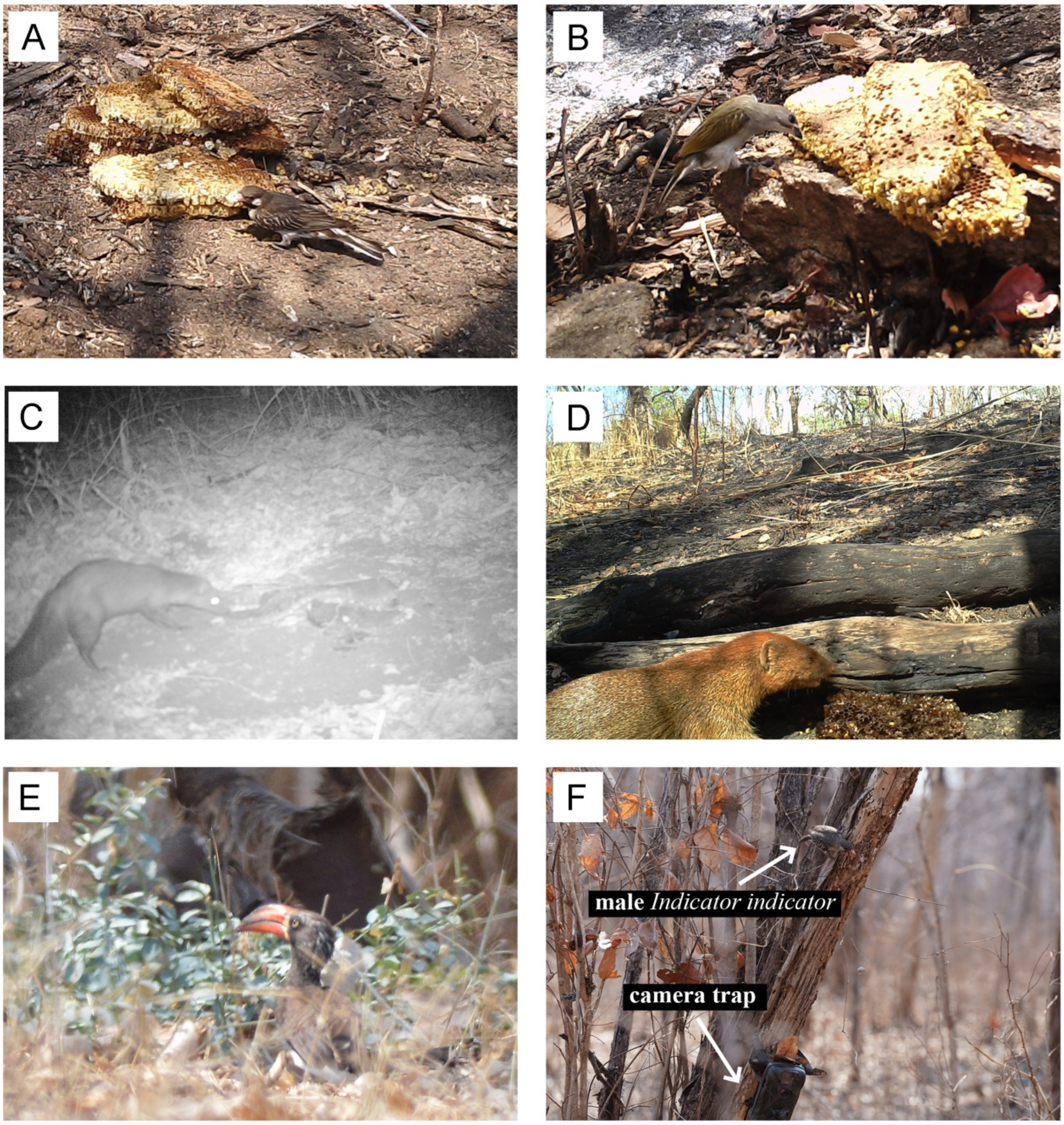


Figure A.3. (A-F) Camera-trap images of animal species eating wax supplementary to figure 1. (A) A male greater honeyguide (*Indicator indicator*) preparing to fly from a pile of wax comb with a small, new piece of wax which it had broken off. (B) Lesser honeyguide (*Indicator minor)* feeding on wax comb containing bee larvae and pupae. (C) Meller's mongoose (*Rhynchogale melleri*) feeding on wax comb nocturnally. (D) Slender mongoose (*Herpestes sanguineus*) feeding on wax comb diurnally. (E) Crowned hornbill (*Tockus alboterminatus*) feeding on wax on the ground. Image taken with a DSLR camera by David Lloyd-Jones. (F) Male greater honeyguide preparing to fly down to a wax pile at ground level whilst ignoring a camera trap < 1 m away.

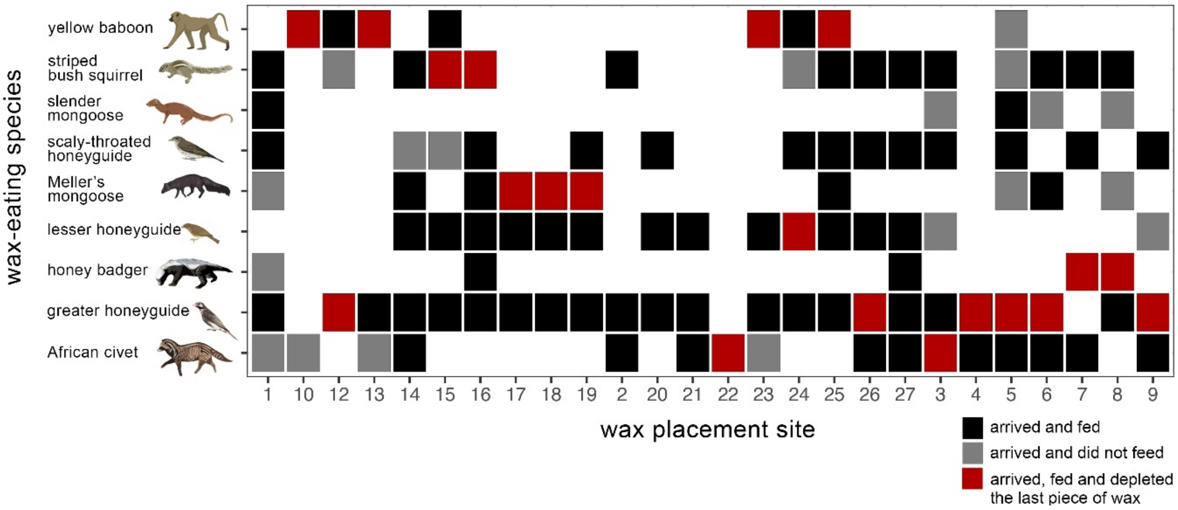


Figure A.4. Arrival of wax-eating species by site. Coloured grid squared indicate whether or not a species was recorded arriving at a wax site and the colour of the square indicates whether that species arrived and fed (black), arrived but did not feed (i.e., arrived after all the wax was depleted; grey) or arrived, fed, and was the species to deplete the last piece of wax at that site (red). For sites with no red square the final animal to feed was unknown.

APPENDIX to CHAPTER 4

Figure A.5. Dead greater galago (*Otolemur garnettii*), to which I was guided to by a honeyguide on 13 June 2018 (photograph by David Lloyd-Jones).

Supplementary text: Account of a 'false positive' report of being guided to a snake

On 11 June 2023, David Lloyd-Jones, Claire Spottiswoode, three honey-hunters and one other researcher, were guided at 0955 h by a juvenile male greater honeyguide. We followed the honeyguide, who produced stereotypical, vigorous 'chatter' calls throughout for 230 meters, and upon reaching a large (> 15 m high) *Ficus bussei* tree, lost sight of the bird but could still clearly hear it chattering in the canopy ahead of us. The habitat was riverine scrub with a nearly closed-canopy at a height of 4–5 m. Most of the group passed the large *Ficus bussei* (continuing to follow the honeyguide ahead) before one of the honey-hunters alerted the group to a Mozambique spitting cobra (*Naja mossambica*) basking by the *F. bussei*. The snake remained fully visible for c. 10 s before entering a tree cavity, allowing us time to identify it. The honeyguide could be heard giving chatter calls ahead of us at this time, but did not go silent at the location of the snake, nor visibly fly downward toward it. We spent 2 minutes 50 seconds at the tree then continued to follow the honeyguide onward for 14 min and 273 m walking distance, whereupon the honeyguide went silent. From that location we could see a large baobab tree (*Adansonia digitata*) 79 m ahead, containing two large bee colonies. At the time, none of the honey-hunters mentioned that the honeyguide had deliberately guided us to the snake. After finding the bees we questioned the honey-hunters for their interpretation of the honeyguide's behaviour and they reported: "the honeyguide paused [at the big tree] therefore it deliberately guided us there". However, considering that the honeyguide did not descend from the canopy, did not go silent at the snake, and subsequently guided us with chattering calls to a tree with bees 273 m away, we infer that the honeyguide did not deliberately guide us to this snake.

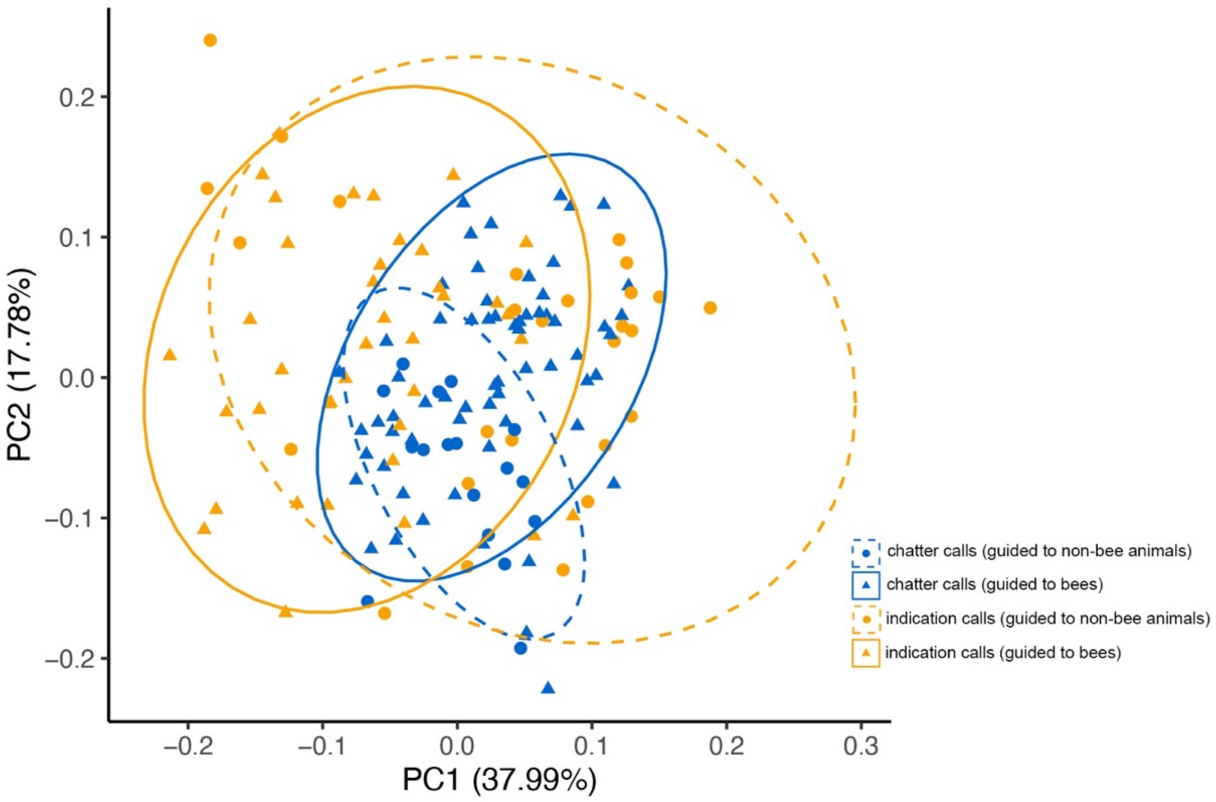


Figure A.6. Results of a principal components analysis (PCA) comparing the acoustic parameters of two types of honeyguide sounds given whilst guiding: (1) 'chatter' calls typically given by the honeyguide when guiding to a bees' nest (blue points with ovals indicating 95 % confidence levels), and (2) 'indication' calls given by the honeyguide as they near the location of a bees' nest when guiding (yellow points with lines indicating 95 % confidence levels). Honeyguide 'chatter' and 'indication' calls are generally distinctive from each other, with some syllables of the 'chatter' calls generally intermingled with distinctive squeaky 'indication' syllables (Isack, 1987). There is a high degree of overlap between 'chatter' calls en route to bees' nests, and en route to animals other than bees (blue points). These are somewhat separate to 'indication' calls, which also overlap regardless of whether they are given en route to bees' nests or en route to animals other than bees (yellow points). All recordings were made in the course of this study; datapoints are individual syllables from the calls of n = 6 honeyguides en route to bees' nests, and n = 2 honeyguides en route to animals other than bees.

Table A.2. Acoustic parameters measured using 'warbleR' package in R, to compare 'chatter' and 'indication' calls emitted by honeyguides. Parameters in **bold** were not used in the principal components analysis (PCA) as they were highly correlated ($R^2 > 0.75$) with other variables.

Measure	Description
duration	length of signal (in s)
meanfreq	mean frequency (in kHz). Calculated as the weighted average of the frequency spectrum (i.e. weighted by the amplitude within the supplied band pass)
sd	standard deviation of frequency (in kHz). Calculated as the weighted SD of the frequency spectrum
freq.median	median frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of equal energy (in kHz)
freq.Q25	first quartile frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of 25% and 75% energy respectively (in kHz)
freq.Q75	third quartile frequency. The frequency at which the frequency spectrum is divided in two frequency intervals of 75% and 25% energy respectively (in kHz)
freq.IQR	interquartile frequency range. Frequency range between 'freq.Q25' and 'freq.Q75'
time.median	median time. The time at which the time envelope is divided in two time intervals of equal energy (s)
time.Q25	first quartile time. The time at which the time envelope is divided in two time intervals of 25% and 75% energy respectively (s).
time.Q75	third quartile time. The time at which the time envelope is divided in two time intervals of 75% and 25% energy respectively (s)
time.IQR	interquartile time range. Time range between 'time.Q25' and 'time.Q75' (s)
skew	skewness. Asymmetry of the frequency spectrum
kurt	kurtosis. Peakedness of the frequency spectrum
sp.ent	spectral entropy. Energy distribution of the frequency spectrum. Pure tone ~ 0; noisy ~ 1.
time.ent	time entropy. Energy distribution on the time envelope. ~0 means amplitude concentrated in a specific time point, 1 means amplitude equally distributed across time
entropy	spectrographic entropy. Product of time and spectral entropy sp.ent * time.ent.
sfm	spectral flatness. Similar to sp.ent (Pure tone ~ 0; noisy ~ 1).
meandom	average of dominant frequency measured across the spectrogram
mindom	minimum of dominant frequency measured across the spectrogram
maxdom	maximum of dominant frequency measure across the spectrogram
dfrange	range of dominant frequency measured across the spectrogram
modindx	modulation index. Calculated as the cumulative absolute difference between adjacent measurements of dominant frequencies divided by the dominant frequency range (measured on the spectrogram)
startdom	dominant frequency measurement at the start of the signal (measured on the spectrogram)
enddom	dominant frequency measurement at the end of the signal (measured on the spectrogram)
dfslope	slope of the change in dominant frequency (measured on the spectrogram) through time
peakf	peak frequency. Frequency with the highest energy and is measured on the frequency spectrum.
meanpeakf	mean peak frequency. Frequency with highest energy from the mean frequency spectrum
meanfun	average of fundamental frequency measured across the acoustic signal
meanfun	average of fundamental frequency measured across the acoustic signal
minfun	minimum fundamental frequency measured across the acoustic signal
maxfun	maximum fundamental frequency measured across the acoustic signal
hn_freq	mean frequency of the 'n' upper harmonics (kHz) (see analyze). Number of harmonics is defined with the argument 'nharmonics'. Only measured if harmonicity = TRUE.
hn_width	mean bandwidth of the 'n' upper harmonics (kHz)
harmonics	the amount of energy in upper harmonics, namely the ratio of total spectral power above 1.25 x F0 to the total spectral power below 1.25 x F0 (dB)
HNR	harmonics-to-noise ratio (dB). A measure of the harmonic content