Begging Call Mimicry and Host Manipulation by Brood-Parasitic Honeyguides

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Dissertation presented for the degree of

Master of Science

FitzPatrick Institute of African Ornithology

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April 2024

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Abstract

Brood-parasitic birds lay their eggs in the nests of other species ('hosts'), and their chicks encounter the challenge of acquiring sufficient food from host parents. Many parasitic chicks require more food than host chicks, and so need to elicit high rates of provisioning through their begging displays. Greater (*Indicator indicator*) and lesser (*I. minor*) honeyguides are closely related brood parasites that require more food than host chicks, whom they kill soon after hatching. Previous research demonstrated that both species receive the same amount of food as an entire brood of hosts (little bee-eaters *Merops pusillus* and black-collared barbets *Lybius torquatus* respectively), and that their begging calls influence provisioning by host parents. However, the acoustic mechanisms facilitating this phenomenon remained unknown. In this dissertation, I first test whether greater and lesser honeyguides mimic the begging calls of their respective hosts and quantify the accuracy of acoustic mimicry. I then test the hypothesis that honeyguides elicit increased provisioning from host parents by mimicking an entire brood of host chicks. I found that while both honeyguides mimic their host's nestlings, they do not specifically replicate the sound of a brood rather than a single chick. Finally, I test the hypothesis that non-linear vocal phenomena (NLP) in honeyguide begging calls could facilitate a supernormal stimulus particularly when the pitch and temporal structure of begging calls is constrained (such as by selection for mimicry). NLP are known to indicate high-arousal states in other ecological settings, inspiring the hypothesis that elevated NLP could function to increase provisioning to parasitic chicks beyond levels individual host nestlings would receive. I found that greater honeyguides tended towards higher perceived roughness (a form of NLP) than single bee-eater nestlings, but not significantly so. Lesser honeyguide begging calls tended towards higher amplitude modulation frequencies and perceived roughness than single barbet nestlings, but this too was not significant. Since both these features are associated with the amplitude envelope, I conducted a playback experiment at black-collared barbet nests in the field in Zambia to test whether the shape of the amplitude envelope of honeyguide begging calls increases host provisioning. This cautiously suggested it did not, at least at the levels manipulated here. Together, these results show that honeyguides mimic the pitch and temporal structure of their primary hosts' begging calls but do not mimic a brood to increase host provisioning, contrary to previous suggestions. The results are inconclusive as to whether NLP could be exploited by honeyguides to increase host provisioning. NLP should be further examined as a potential signalling mechanism that could be exploited by brood parasites to elevate the level of provisioning by host parents. More generally, the signalling function of NLP in bird begging calls, which had not been examined prior to this dissertation, deserves further investigation.

Acknowledgements

I am deeply indebted to the many individuals who have supported, guided, and collaborated with me throughout the process of completing this dissertation.

First and foremost, I extend great appreciation to my supervisors, Claire Spottiswoode and Jess Lund, from whom I have learnt an enormous amount and who have been so kind, supportive, and inspiring throughout this process. I have had the privilege to be supervised by Claire for both my Honours and MSc research and her genuine passion and skill for thinking about and uncovering the processes of the natural world is inspirational. I thank Jess for always being available to offer her sharp scientific mind to talk through and provide clarity to ideas, which has been invaluable throughout the process of writing this dissertation. I also greatly appreciate Jess's patience and sense of humour when teaching me the ropes in the field and her understanding of my chaotic ways.

I am grateful to the University of Cape Town for their offer of the VC Masters Scholarship, which covered my registration and living fees in Cape Town. I am also grateful to the DST-NRF Centre of Excellence at the FitzPatrick Institute for providing funding for the fieldwork in Zambia.

I extend thanks to Hilary Buchanan, Anthea Links, and Susan Miller for all their help with administrative and bureaucratic tasks, and for all the tearoom chats. I am grateful for the friendship and empathy provided by the other students at the Fitz, particularly Koi Pillay, Joel Radue, Robi Watkinson, Abbey Campbell, Mpho Munyadziwa, Obakeng Pule, Kyle Walker, and Rebecca Muller.

Emmanouela Rantsiou's collaborative help, using her coding and mathematics skills to create the python code which I used with the sound manipulations for the playbacks, was essential to the playback experiments and I am indebted to her for this. I am also grateful for the enthusiasm and patience with which she shared her extensive knowledge of the physics of sound with me. I learnt so much through our discussions which informed much of my understanding when conducting this research. A special thanks must be extended to Lakshminarayanan Mahadevan for providing of his time to offer his physics and maths mind to provide fresh insights into the ways birds may manipulate their calls.

Luke McClean's foundational work on brood parasitism in honeyguides laid the groundwork from which the ideas for this work were formed and I am grateful for his enthusiasm about this work and willingness to provide additional begging call recordings.

I am thankful for the Choma community for being so welcoming during my time in Zambia. Particularly, I would like to thank Molly and Archie Greenshields for allowing us to stay at their beautiful home in the Miombo and providing us with such delicious food; Richard and Vicki Duckett, Troy and Elizabeth Nicolle, Ackson Sejani and James Ndambo for their permission to work on their farms and support our work; and Emma and Ian Bruce-Miller, Mary Counsell, Shaina Irwin and Matthew, Bruce, Patrick and Sandy Danckwerts for their hospitality while in I was in Choma. I also thank Dewis Hamapa, the farm manager at Masistah's, for his permission to look for

barbet nests for the playback experiments on the Masistah’s farm at such short notice.

I would like to thank the other researchers, Matt Lobenhofer, Mairenn Attwood, Chima Nwaogu, Johah Walker, Gabriel Jamie and Maggie Mwale who provided friendship and support while in the field and made the time in the field infinitely more enjoyable. I thank Tanmay Dixit for the opportunity to assist in collecting data for his PhD, which allowed me to visit and become acquainted with the field site before I started my field season, which proved to be incredibly useful when planning and conducting my own fieldwork. I thank Silky Hamama, Collins Moya and Onest Siakwasia, the primary field assistants, for their companionship through long days in the field and incredible skill and care in accessing nests. Without the remarkable skill of the nest finder team to find nests, none of this work would have been possible, and I am incredibly grateful for their help locating nests.

I thank my parents, Mark and Wendy Blair, for nurturing and supporting my passion and love of birds from a young age right through to today. I am so grateful as well for my partner, Vidal Thaver, who has been supportive and understanding to me throughout the whole process and I feel very lucky to have had her by my side.

Lastly, I thank the barbets, bee-eaters, and honeyguides from which I have learnt so much, but, more importantly, have realised that there is so much more than needs to be understood about the lives of these fascinating birds.

Funding and permits

The fieldwork expenses for this project were funded by the DST-NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology and registration fees were funded by a UCT VC Masters Scholarship. The methods used in this dissertation were approved by the University of Cape Town's Science Faculty Animal Ethics Committee (approval number: 2022/V15/CS). The fieldwork conducted for this dissertation was conducted on private land in Zambia with permission by all landowners and under a research permit granted by the Zambian Department of National Parks and Wildlife (permit number: DNPW/8/27/1).

Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

Signed:

Date: 2 April 2024

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CHAPTER 1

Introduction

Avian brood parasites lay their eggs in the nests of other birds, and therefore their chicks are raised by a different species. How do these chicks trick their host parents into feeding them enough? In this dissertation I explore how parasitic chicks can use mimicry of begging vocalisations to manipulate the behaviour of their host parents and suggest other manipulative mechanisms that brood parasites may use. In this introductory chapter, I provide a theoretical background to (i) biological mimicry and how to test it, (ii) begging call signal design, and (iii) host parent manipulation by brood-parasitic nestlings, including when to expect it and how it may develop. I examine two broad mechanisms that brood parasites may use to manipulate host parents: brood mimicry, and supernormal stimulation of need signals. I then propose hypotheses for how two closely-related brood parasites, the greater honeyguide (*Indicator indicator*) and lesser honeyguide (*I. minor*), are able to overcome the challenges of avoiding detection and obtaining sufficient provisioning.

1.1 Biological mimicry and how to test it

1.1.1 What is mimicry?

Biological mimicry has resulted in some of the most remarkable phenotypes exhibited by living organisms. It has led to caterpillars that resemble snakes (Hossie & Sherratt, 2013), snakes with tails that resemble spiders (Fathinia et al., 2015), and orchid flowers that resemble bees, wasps, and beetles (Cohen et al., 2021; Schiestl & Cozzolino, 2008; Steiner, Whitehead & Johnson, 1994) among many other extraordinary examples. Vane-Wright's (1980) classic definition of mimicry states that mimicry "involves an organism (the mimic) which simulates signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the receiver), such that the mimic gains in fitness as a result of the receiver identifying it as an example of the model". This definition was updated by Dalziell, Welbergen & Magrath (2014), who consider mimicry to occur "if the behaviour of the receiver changes after perceiving the resemblance between the mimic and the model, and the behavioural change confers a selective advantage on the mimic.".

Organisms do not only mimic signals, which are given specifically to alter the behaviour of the receiver, but can also mimic cues, defined as incidental information detected by unintended receivers (Jamie, 2017; Maynard Smith & Harper, 2003). For example, fork-tailed drongos (*Dicrurus adsimilis*) mimic the alarm calls of other species, in order to scare animals away from their food and steal it (Flower, Gribble & Ridley, 2014). Alarm calls are both signals when received by conspecifics and cues when received by heterospecifics. Therefore, when a drongo uses the alarm call of one species to steal food from another species, it is exhibiting cue mimicry (Jamie, 2017). Organisms may even mimic inanimate objects, termed masquerade, which is a special case of cue mimicry (Jamie, 2017). For example, some caterpillars mimic bird droppings to avoid predation (Cott, 1940). However, in each of these cases, mimicry occurs as the result of there being selective advantage on the mimic, as a result of a behavioural change in the receiver. Therefore, this criterion is crucial for detecting whether mimicry is occurring (Dalziell, Welbergen & Magrath, 2014).

1.1.2 How can mimicry be tested?

To find evidence of mimicry in a particular system, first the mimic needs to exhibit similarities to salient features of the model signal or cue from the perspective of the receiver (Dalziell, Welbergen & Magrath, 2014; Jamie, 2017). In most mimetic systems, mimicry is imperfect, with varying degrees of fidelity to the model (Kikuchi et al., 2013; Sherratt, 2002). It is important to measure similarity between models and mimics in a receiver-appropriate way because the receiver's sensory systems may differ substantially from our own. In some cases, model and mimic signals or cues may appear to us to be very dissimilar, but the receiver may nonetheless perceive them as similar (Dixit et al., 2023; Sherratt, 2002). Second, the receiver needs to respond similarly to the stimuli of the model and the mimic (Dalziell, Welbergen & Magrath, 2014). It is therefore essential to consider the sensory systems of the receivers when assessing whether mimicry is occurring (Dalziell, Welbergen & Magrath, 2014; De Jager & Anderson, 2019).

Mimicry is only one of several processes that can generate similarity (De Jager & Anderson, 2019; Grim, 2004). Other causes of resemblance between taxa are convergent evolution, common descent, gene flow, crypsis, pleiotropy, or chance (De Jager & Anderson, 2019; Grim, 2004). For mimicry to be accepted as the cause of resemblance between organisms, the other possible mechanisms that may lead to resemblance must be excluded (De Jager & Anderson, 2019). If the signals of the mimic are closer to those of the model than to those of its closest relatives, this may additionally provide support for the hypothesis that a resemblance is due to mimicry rather than common descent (Jamie et al., 2020; Jønsson et al., 2016).

1.1.3 Mimicry in brood-parasitic systems

Brood parasites are animals which pass on parental duties to other animals and are therefore freed from the costs of parental care. Brood parasitism has been most widely studied in birds, but also occurs in various insects and a fish species (Sato, 1986; Spottiswoode, Kilner & Davies, 2012). Across brood parasites, mimicry is common, and brood parasites mimic signals and cues across a variety of sensory modes which include acoustic, visual, and olfactory information (Grim, 2005; Jamie & Kilner, 2017). Mimicry offers an effective mechanism whereby brood parasites evade detection by their hosts and ensure that they receive adequate parental care (Jamie & Kilner, 2017). Since both are necessary for the survival of a brood parasite, selection for mimicry may be strong. In avian brood parasites, mimicry of egg phenotypes and nestling begging displays are the most commonly observed types of mimicry (Jamie & Kilner, 2017; Langmore & Spottiswoode, 2011). Brood-parasitic mimicry has often evolved in response to mechanisms developed by the host to identify foreign eggs or nestlings, often as a result of coevolution between host defences and parasitic counter-adaptations (Mársico, 2012; Soler, 2013; Stoddard & Hauber, 2017). For example, fork-tailed drongos are parasitised by African cuckoos (*Cuculus gularis*) and have evolved the ability to recognise and reject dissimilar eggs from their nests (Lund et al., 2023). This in turn has selected for high-fidelity mimicry of host eggs by the cuckoo (Lund et al., 2023). In turn, drongos have been able to effectively counteract the high-fidelity mimicry by cuckoos by diversifying their own egg phenotypes (Lund et al., 2023).

Mimicry of host begging calls by brood parasites may evolve to ensure they are adequately provisioned and/or not rejected by their host parents. Begging calls are used by bird nestlings to beg for food from parents or host parents and are present across the entire radiation of birds (Wright & Leonard, 2002). Similarity between the begging calls of host and parasite chicks has been identified in many systems (Jamie & Kilner, 2017). However, in most cases, it has only been subjectively assessed, and quantitative methods have only been used to assess the similarity between brood parasites and their hosts in a few systems (Jamie & Kilner, 2017). As mentioned above, resemblance alone does not provide enough evidence for mimicry, and other possible reasons for similarity need to be excluded, and an investigation into the behavioural responses of the receiver to relevant stimuli, and how these behavioural responses may impose selection on the mimic, is essential to demonstrate that mimicry is occurring (Dalziell, Welbergen & Magrath, 2014; De Jager & Anderson, 2019).

Brood mimicry, mimicry of cues associated with the begging of multiple host nestlings in the nest, may be exhibited by brood parasites that evict the host chicks from the nest and are raised alone (Davies, Kilner & Noble, 1998; McClean, 2020). This is because the needs of the brood-parasitic chick may exceed those of the host's own nestlings (Davies, Kilner & Noble, 1998; Jenner, 1788; McClean, 2020). Mimicking cues associated with broods of host chicks allows the single parasitic nestling to be provisioned at a level equivalent to that of a brood of hosts (Butchart et al., 2003; Davies, Kilner & Noble, 1998). Therefore, mimicry may be used by brood parasites both to avoid detection, and to manipulate the provisioning behaviour of their host parents.

Host-specific begging call mimicry can provide a challenge to achieve because these host-specific adaptations need to be expressed in both male and female chicks. This differs from host-specific egg mimicry of generalist brood parasites because the egg phenotype depends on the genetics of the mother. Therefore, whether the egg hatches into a male or female chick, it is possible for host-specific egg phenotypes to be passed down directly from mother to daughter, likely via the W chromosome (Spottiswoode, 2011). This allows females that specialise on different hosts, and lay eggs mimicking those respective hosts, to exist within the same species (Jensen, 1966; Punnett, 1933). However, the chick phenotype depends on the genetic makeup of the chick itself, and host races of chicks cannot be sustained within the same species using the same mechanism. Host-specific begging call mimicry in brood parasites with more than one host species may be achieved through social shaping by the host parents. For example, in Horsfield's bronze cuckoos (*Chrysococcyx basalis*), this is achieved by cuckoo nestlings giving multiple types of calls and adjusting which calls they give based on how effective they are at eliciting provisioning from their host parents (Langmore et al., 2008).

1.2 Begging call design

Before examining further how brood parasites use begging displays to manipulate their host parents, it is important to understand the information begging provides to parents, as well as the development of begging and its constraints.

1.2.1 Information content of begging signals

Begging displays provide information to parents about the amount of food that needs to be provisioned to their chicks (Johnstone & Godfray, 2002). However, whether differences in need are presented in begging calls as a continuous scale of need or discrete levels of different needs states is not well understood, which has implications for parasitic mimicry. (Johnstone & Godfray, 2002). Empirically, it appears that parents are able to adjust their provisioning in response to fine-scale differences in the needs of their chicks, suggesting that need is signalled in a continuous manner (Johnstone & Godfray, 2002). However, models suggest that signalling by chicks for continuous differences in need requires there to be significant costs to dishonest signalling to maintain the reliability of the signal (Johnstone and Godfray, 2002). Otherwise, it would be adaptive to signal dishonestly for a greater amount of food than is needed, which in turn would break down the response to the begging calls by the parents (Johnstone and Godfray, 2002). An alternative is to signal for discrete ranges or pools of conditions, which requires less cost to maintain honesty of the signal and could even remain stable without direct costs (Johnstone and Godfray, 2002). Johnstone and Godfray (2002) demonstrate that it can be maintained by the indirect cost of decreasing parental fitness, by signalling for more resources than the parent is able to provide without expending excessive effort. These discrete pools are however not consistent with what we see in reality, with begging calls and parental response in provisioning both generally varying continuously, indicating that the information content of begging signals is likely on a continuous scale (Johnstone and Godfray, 2002). The resolution of need signalling in brood parasite hosts is important to consider since it influences the range of options available to brood parasites for manipulation of host parents.

However, nestlings are not always honest in their need. In a comparative analysis across 60 species of birds, Caro, West & Griffin (2016) found that offspring were generally less honest about their need for provisioning when they are in conflict in some way with their siblings, either through competition with current or future siblings, or through parental divorce or death meaning that they are less related to future siblings. Therefore, the more chicks present in a brood, the more likely they are to dishonestly signal their need (Caro, West & Griffin, 2016). Whether they are signalling honestly or dishonestly, begging calls provide a signal of nestling need that parents respond to. This leads to the question of which begging call features cause the parents to adjust their provisioning rate.

A number of studies have examined how the begging calls of chicks change depending on their age and condition, as well as how changes in various begging call features influence parental responses. In Table 1.1 below, I summarise some results from these studies which give insights into the features of begging calls that provide useful information to parents, and those that parents respond to. Narrow frequency range, higher peak frequency, higher or lower amplitude, longer or shorter call duration and higher call rate, are each associated with either nestling need or increased parental provisioning in various systems. Each feature therefore represents a candidate that may function to signal nestling need, and so is vulnerable to exploitation by brood parasites.

Table 1.1: Non-exhaustive summary of studies examining changes in begging calls with age and need, and parental responses to these changes. Brood-parasitic species are indicated with an asterisk.

Begging call feature	**Studies demonstrating its value as a signal**	**Species**	**Change**
Frequency	Anderson, 2010	Grey warbler *Gerygone igata*	Frequency range narrowed as hunger increased. Frequency increased with age.
	Sacchi et al., 2002	Barn swallow *Hirundo rustica*	Food deprived nestlings begging calls have a higher peak frequency.
	Hauber and Ramsey, 2003	Brown-headed cowbird *Molothrus ater **	Peak frequency decreased as chicks got older.
Amplitude	Anderson, 2010	Grey warbler *Gerygone igata*	Amplitude decreased with increasing hunger.
	Corney and Barber, 2018	Common starling *Sturnus vulgaris*	Playback of louder begging calls increased provisioning rate.
Temporal composition	Anderson, 2010	Grey warbler *Gerygone igata*	Duration of call elements become shorter with age.

	Sacchi et al., 2002	Barn swallow *Hirundo rustica*	Food deprived nestlings beg more frequently, with longer call elements.
	Kilner, Noble & Davies, 1999; Buchart et al., 2003	Common cuckoo *Cuculus canorus* *	Adjusts call rate depending on host species but structure remains similar. Increased call rate associated with increased host provisioning rate.
	Hauber and Ramsey, 2003	Brown-headed cowbird *Molothrus ater* *	Higher rate of begging bouts with increased hunger level.
	Gloag and Kacelnik, 2013; Ursino et al., 2018	Shiny cowbird *Molothrus bonariensis* *	Tremulous calls are very different to calls of single house wren (*Troglodytes aedon*) chicks, their hosts. These tremulous calls increase the provisioning rate of the host parents, likely as a result of higher call rate.

1.2.2 Nonlinear vocal phenomena as a potential signal of need in begging calls

The begging call features discussed in Table 1.1 describe the pitch, loudness, or temporal arrangement of elements, but it is likely that there are other features that could signal nestling need to host parents. For example, the studies have so far neglected the possibility that timbre or perceived quality of begging calls could be a signal of nestling need in birds. The timbre of a call is affected by the harmonic structure and the presence of amplitude modulation. Specifically, harsher or rougher calls may signal higher need states in bird begging calls. In animal vocalisations, rough or harsh sounding calls are the result of non-linear vocal phenomena (NLP).

NLP are deviations from regular tonal vocal production resulting from the perturbations in the typical rhythmic vibration of the vocal folds (Anikin et al., 2020). To humans, NLP lower perceived voice pitch, increases voice darkness and roughness, and causes the vocaliser to sound larger, more formidable, and more aggressive (Anikin, 2021). NLP have been best studied in mammal vocalisations, particularly distress vocalisations. For example, NLP signal the level of distress in the vocalisations of infant humans, chimpanzees, bonobos, and deer, and likely many other mammals (Lingle et al., 2012; Techroeb et al., 2013; Thévenet et al, 2023). In most contexts in which it is displayed, higher degrees of NLP appear to signal high arousal levels.

In birds, NLP are poorly studied. NLP are present in the vocalisations of many birds, but little work has been done on its potential for signalling arousal level. Some studies have found that birds respond to NLP by becoming more alert (Blesdoe and Blumstein, 2014; Slaughter et al., 2014), and nonlinear dynamics can contribute to greater complexity in bird songs which can be created by a small number of simple neural signals (Fee et al., 1998; Zollinger et al., 2008). Surprisingly, the presence of NLP in the begging signals of birds appears to have not been examined at all, despite being present in analogous signals in mammals. NLP are worth considering as a possible signal of need since it is likely easily manipulated by chicks and is effective at signalling high arousal states in other systems.

1.2.3 Constraints on begging call signals

Understanding the physical and evolutionary constraints on begging calls is important to understand how features of begging calls are able to vary and thus signal to parents. For example, there appears to be a trade-off between frequency range and trill rate in the songs of sparrows and buntings in the Emberizoidea superfamily, with the highest frequency bandwidth observed decreasing with increasing trill rate (Podos, 1997). In this clade, this pattern likely represents a physical constraint that affects the structure of their vocalisations, or a constraint in the perception of receivers (Henry et al., 2011). However, the constraints on trill rate in other birds have not yet been studied.

The structure of begging calls may also be constrained by selection pressures from unwanted eavesdroppers. Specifically, costs may be imposed by loud and exaggerated calls betraying the location of chicks to predators, potentially shaping the evolution of begging calls. Counter-intuitively, predation risk may even explain why many begging displays are so exaggerated and conspicuous: the “blackmail hypothesis” proposes that begging forces parents to provide food to nestlings, so that they remain safe (Thompson et al., 2012).

The structure of begging calls may also be shaped by the nest environment since this affects sound transmission and so the conspicuousness of begging calls. For example, nest environments where sound transmission to the outside of the nest is restricted, such as in a tree hole, are expected to have begging displays with more conspicuous features without being detectable by predators (Soler, 2002). Other characteristics of the nest environment that affect the transmission and reception of sound also likely play an important role in the design of begging calls. In reverberant nests, such as those in tree and ground holes with walls that are solid and hence reflect sound, shorter elements, broader frequency ranges, more directional sounds and a lack of amplitude modulation are generally found (Horn & Leonard, 2001). This is consistent with the idea that nestlings in reverberant nests could use constructive interference from reflected sounds to amplify their calls when calling at specific frequencies (Horn & Leonard, 2001). Nestlings may also use destructive interference to effectively ‘jam’ the calls of their nestmates (Horn & Leonard, 2001).

Another factor that could influence the reception of a sound, and so affect selection on begging calls, is the locatability of the source of the sound. Bird species that have had their ability to locate sound tested are able to locate sounds to a resolution of 20–30 degrees apart (Dooling 1992). Locatability of begging calls is especially important in nest environments that have little light available, such as nests within tree and ground holes. This is because there are no visual cues of nestling location available to the parents. Nestlings with more locatable calls may receive food more often and outcompete their nestmates. This creates selection for call features that increase locatability, such as a broad frequency range (Dooling, 1992; Horn & Leonard, 2001).

Therefore, adaptation to sibling competition, predation risk and to the specific physical environment of the nest may all affect the structure of begging calls, and these selection pressures may also potentially affect brood parasites who share the same nest environment as their hosts. Since begging calls are used by parents to assess the amount of food the chicks require, they are vulnerable to exploitation by brood parasites to manipulate the provisioning behaviour of their host parents by either exaggerating features associated with need, or mimicking cues associated with a brood of nestlings begging together.

1.3 Host manipulation by brood-parasitic nestlings

Many brood parasites have food requirements that differ from those of their host’s nestlings, typically involving higher food requirements owing to larger body size and/or increased growth rate. In this section, I outline how brood parasites can use existing communication systems between parents and their offspring to manipulate their host parents.

1.3.2 Examples of begging signals used to manipulate host parents

The best-known examples of parasites using vocal begging signals to manipulate provisioning by hosts come from the common cuckoo (*Cuculus canorus*), which evicts host chicks from the nest but needs to grow much faster and larger than the nestlings of each of their host species. They therefore need to manipulate the provisioning behaviour of their host parents to achieve this. The common cuckoo has a begging call rate that significantly exceeds that of host nestlings and is comparable to that of a host brood begging simultaneously (Kilner, Noble & Davies, 1999). Common cuckoos parasitise a range of species and adjust their call rate to slightly exceed that of a brood of host nestlings, which compensates for the deficient visual stimulus provided by their single gape (Buchart et al., 2003; Kilner, Noble & Davies, 1999). The structure of the call elements does not differ between hosts, however, suggesting that specifically call rate is an important stimulus that determines the amount of food each host species to provides to its chicks (Buchart et al., 2003). This system of communication is then co-opted by the brood-parasitic cuckoo to manipulate its host parents into feeding it more.

Mimicry of a brood to manipulate host provisioning has not only been found in acoustic stimuli, but also in visual stimuli associated with a larger brood of nestlings. Malaysian hawk-cuckoo (*Hierococcyx fugax*) nestlings have fleshy yellow patches on their wings which mimic the gapes of chicks. This makes it look like there are more chicks in the nest, and tricks host parents into increasing their provisioning rate (Tanaka and Ueda, 2005).

Eliciting higher provisioning rates from host parents also occurs in non-evicting brood parasites, most famously in the cowbirds (*Moluthrus* spp.) of the Americas. In brown-headed cowbirds (*Molothrus ater*) parasitising prothonotary warbler (*Protonotaria citrea*), provisioning rate was significantly higher in nests with cowbirds present (Hoover and Reetz, 2006) after controlling for brood mass. This suggests that there is some aspect of the begging display of cowbirds that causes host parents to increase provisioning.

The begging calls of shiny cowbird (*Molothrus bonariensis*) nestlings also seem to have a structure that manipulates at least some species, including some that are not parasitised by cowbirds. Shiny cowbirds are generalists that parasitise over 100 host species. They give a tremulous begging call that differs from the simple calls of nestling house wrens (*Troglodytes aedon*), one of their frequently used hosts, and appears to be similar regardless of the host species. Gloag and Kacelnik (2013) played back cowbird calls to a species completely naïve to cowbird parasitism (great tits *Parus major*) and found that they were more responsive to the cowbird calls than to their own chicks. It is not always effective, however: in baywings (*Agelaioides badius*), which are parasitised by both screaming cowbird (*Molothrus rufoaxillaris*) and shiny cowbird, shiny cowbird calls do not increase provisioning rate (Ursino et al., 2018). In contrast, the calls of screaming cowbirds, which are specialist parasites of baywings, do increase the provisioning rate of baywings since the structure of their calls more closely resembles that of the baywing nestlings (Ursino et al., 2018). Therefore, in some systems, host-specific mimicry is required to be effective at obtaining sufficient provisioning.

Deceptive begging signalling is not restricted to birds. For example, the brood-parasitic larvae of the beetle *Atameles pubicollis*, which reside in colonies of *Formica polyctena* ants, beg more intensely than the ant larvae and obtain more food. They beg not through visual and acoustic signals, but mechanical signals, stimulating the labium of the ant to obtain food (Holldobler and Wilson, 1990). Acoustic signals are even used by at least one insect social parasite, a butterfly caterpillar (*Maculinea* *rebeli*) that mimics the sounds of queen ant (*Myrmica schencki*) to achieve high status within the ant colony (Barbero et al., 2009).

1.3.3 Brood mimicry or supernormal stimulation?

Two hypotheses have been suggested to explain how brood-parasitic birds may manipulate their hosts using begging calls: (i) brood mimicry and (ii) supernormal stimulation (Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2013; Kilner, Noble & Davies, 1999). In brood mimicry, the elevated provisioning response from the host parent results from the perceived similarity between cues they associate with a higher number of hungry nestlings, and the signals given by nestling brood parasites. In the above examples, the host parents of common cuckoos and Malaysian hawk cuckoos likely respectively associate higher call rates and more yellow skin with more nestlings that need food (Davies, Kilner & Noble, 1998; Tanaka and Ueda, 2005). The parasites then exploit this response by the host parent by mimicking these cues.

Alternatively, brood parasites may exaggerate features that signal need in begging displays, which results in supernormal stimulation (Dearborn & Liechtenstein, 2002; Kilner, Noble & Davies, 1999). When host parents adjust their provisioning in response to particular begging call features that signal need, brood parasites are able to manipulate their rate of provisioning by exaggerating these features. In the examples above where brood parasites manipulate host parent provisioning, both brood mimicry and supernormal stimulation of features associated with need have been suggested as possible mechanisms of host manipulation. However, it is unclear in these cases which mechanism is responsible for increased host provisioning since this has not been specifically tested.

1.4 Honeyguides as brood parasites that manipulate their hosts

One group of brood parasites where manipulation of host parent provisioning has been demonstrated is the honeyguide family (Indicatoridae) (Short and Horne, 2001). Two species, the greater honeyguide (*Indicator indicator*) and lesser honeyguide (*Indicator minor*) are the most widespread and abundant honeyguide species across Africa. They both parasitise hole-nesting birds (Short and Horne, 2001). In greater honeyguides, there are two ancient, genetically distinct maternal lineages (Spottiswoode et al., 2011). One lineage parasitises birds that nest in tunnels that have been dug into the ground (Spottiswoode et al., 2011) (e.g. little bee-eaters *Merops pusillus*, swallow-tailed bee-eaters *M. hirundineus*, and grey-headed kingfishers *Halcyon leucocephala*). The other lineage parasitises birds that use cavities in trees or the ground (e.g. African hoopoe *Upupa africana*, green woodhoopoe *Phoeniculus purpureus*, common scimitarbill *Rhinopomastus cyanomelas* and striped kingfisher *Halcyon chelicuti*). These holes may be excavated by the host itself, be a nest previously excavated by another species, or have arisen through some other means (Spottiswoode et al., 2011). Lesser honeyguides almost exclusively parasitise African barbets (Family Lybiidae), which excavate nest holes in dead branches of trees (Short & Horne, 2001). There have been reports of them parasitising other birds that use tree holes to nest, but these may be misidentifications and use of other species appears to be rare at best (Short & Horne, 2001). Begging calls of greater honeyguides within the nests of little bee-eaters and lesser honeyguides within the nests of black-collared barbets were well described by McClean (2020). However, few publicly available begging call recordings exist of these honeyguides in the nests of other host species.

Both lesser and greater honeyguides hatchlings kill the host hatchlings by puncturing and grabbing onto the host hatchlings using sharp hooks on the tip of each mandible (Spottiswoode and Koorevaar, 2012). This results in the honeyguide chick being raised without any nestmates. In both greater and lesser honeyguides, a single honeyguide nestling requires more food than a single host nestling of their primary host, but for different reasons (McClean, 2020). Greater honeyguides are larger than their primary host, the little bee-eater, and therefore their nestlings need to grow faster than the nestlings of their host. Thus, greater honeyguide nestlings need to be fed at a higher rate (McClean, 2020). Lesser honeyguides grow at a similar rate to their host nestlings but require more food because the food they receive from their host parents is suboptimal for their growth (McClean, 2020). Their primary host, the black-collared barbet (*Lybius torquatus*), feeds their nestlings a diet of predominantly fruit, whereas the optimal diet of lesser honeyguides consists mainly of insects and, as adults, bees' wax (McClean, 2020).

Front-line and egg-stage defences against greater and lesser honeyguides are present in both their respective primary hosts. Little bee-eaters mob adult greater honeyguides, and also reject some parasitised clutches (Tong et al., 2015). However, the presence of a honeyguide near a bee-eater nest is not sufficient for bee-eater parents to reject the nest, due to the high costs of nest rejection (Tong et al., 2015). Little bee-eaters do not discriminate between their own eggs and the eggs of honeyguides, and must use additional cues, such as the presence of punctured eggs in the nest, to trigger rejection (McClean, 2020). However, interestingly, female honeyguides do discriminate between bee-eater eggs and honeyguide eggs, and will preferentially puncture the eggs of other honeyguides that have been previously laid in the nest. This imposes selection for egg size mimicry (Spottiwoode, 2013). Black-collared barbets also aggressively mob adult lesser honeyguides near their nests, and often reject or abandon parasitised clutches. Black-collared barbets are more likely to reject parasitised clutches when the lesser honeyguide egg is smaller than their own (McClean, 2020). In both host species, there is a relatively long incubation and nestling period and short breeding season (McClean, 2020). Both honeyguide species have a nesting period even longer than that of their hosts, and usually remain in the nest for 40 days. Therefore, the chances to renest in a season are low, suggesting that there should be high selection pressures for mechanisms to detect parasitism (Langmore & Spottiswoode, 2012).

Since both these honeyguide species parasitise hole-nesting birds, the lack of light inside the nest chamber means that it would be difficult for the hosts to discriminate between their own eggs and chicks, and those of honeyguides. Therefore, hosts would need to use sensory modalities other than vision to detect whether their nests have been parasitised. Begging displays contain acoustic signals that hosts could plausibly use to detect whether they have been parasitised. In hole-nesting species, it is likely that acoustic signals are important in identifying parasitic chicks. Honeyguides, therefore, may need to mimic features of the host's begging call to avoid detection and receive enough food.

However, since honeyguides need more food than host chicks, mimicking host chicks is not enough. They need to manipulate their hosts into feeding them more food than the hosts would feed one of their own nestlings. McClean (2020) showed that for both honeyguide species, the number of feeding visits made to each honeyguide nestling is similar to that provided to a whole host brood. Brood mimicry has been suggested as the most likely mechanism that honeyguides use to increase provisioning by their host parents (McClean, 2020). However, this has only been suggested through a subjective assessment of what the begging calls of honeyguides and their hosts sound like and has not been assessed quantitatively (Fry, 1974; Jubb, 1966; McClean, 2020). It may be that honeyguides actually use supernormal stimulation to manipulate their hosts.

Greater honeyguides are famed for their cooperative relationship with people, where they guide honey hunters to bees' nests using a chattering "guiding call" used only for this purpose (Isack & Reyer, 1989). Acoustic similarity between elements of begging and guiding calls suggests that these calls may even be developmentally related to each other, with guiding calls representing an extension of the begging call into adulthood (Blair et al. MS). Therefore, understanding the processing that shape begging call structure may even have implications for the structure of the guiding call.

1.5 Overview of chapters

The overall aim of this dissertation was to test for evidence of host mimicry in begging calls of honeyguides, as well as to investigate the possible mechanisms by which honeyguides use their begging calls for host parent manipulation.

In Chapter 2 I assess the evidence for begging call mimicry by measuring similarity metrics and comparing each honeyguide species to the other and to their respective primary host species. I also measure and compare features associated with the spectral and temporal structure of the begging calls to examine which features may be cues of the number of hungry host nestlings, or signals of need, both of which may be exploited by honeyguides to manipulate host provisioning.

In Chapter 3 I examine whether the presence of NLP may function as a signal of need in host begging calls that honeyguide nestlings can exploit, without altering the pitch or temporal structure of their vocalisations. I measure features associated with NLP on begging call recordings and compare these between honeyguides and their hosts. I also present the results of a playback experiment where I manipulate the amplitude envelope of the begging calls of lesser honeyguide and their primary host, black-collared barbet, to assess whether amplitude modulation, one type of NLP, affects the provisioning response by barbet parents.

In Chapter 4 I then synthesise the results of the two previous chapters and examine their implications for our understanding of host manipulation by brood parasites, and begging call structure more generally. Additionally, I explore the limitations and future directions of this research.

1.6 Study system and study site

Begging calls were recorded and playback experiments conducted at my research team's long-term field site in the Choma District of the Southern Province of Zambia, predominantly on Semahwa and Musumanene farms which are located approximately 10–15 km west to north-west of the town of Choma. The habitat at the study site is a mosaic of miombo woodland dominated by *Brachystegia, Julbernardia* and *Uapaca* trees, agricultural land (tobacco, tree nut and passion fruit cultivation, and cattle pasture) with interspersed clumps of dense bush centred on termite mounds, and seasonally flooded grassy depressions ("dambos").

At the study site, both greater and lesser honeyguides occur relatively abundantly (although adult greater honeyguides are infrequently seen), and their primary hosts are little bee-eaters and black-collared barbets, respectively. Black-collared barbets (hereafter "barbets"), excavate nest holes in dead branches of large trees. Little bee-eaters (hereafter "bee-eaters") excavate tunnels in the ground that lead to a nest chamber. These tunnels are dug in earth banks or the sides of aardvark (*Orycteropus afer*) burrows, the latter being the favoured site. The main breeding season of both host species is the dry spring season (approximately September–November). At the study site, secondary hosts are also used by both honeyguide species. Greater honeyguides also parasitise African hoopoe (*Upupa africana*), green woodhoopoe (*Phoeniculus purpureus*), common scimitarbill (*Rhinopomastus cyanomelas*), striped kingfisher (*Halcyon chelicuti*) and grey-headed kingfisher (*Halcyon leucocephala*). Lesser honeyguides also parasitise Zambian (*Lybius chaplini*) and crested barbets (*Trachyphonus vaillantii*).

Barbet and bee-eater nests were located by a team of nest finders, who live and work on the farms. Three primary field assistants, Silky Hamama, Collins Moya and Onest Siakwasia assisted with checking the status of nests using a Ridgid CA-25 endoscope (Emerson Electric Company, St Louis, USA) and accessing nests. Accessing barbet nests was achieved by using an adze to cut a small square piece of wood along the branch at the nest chamber to create a "door" which can be removed to access the contents of the nest, then replaced and secured with wire so that the nest chamber remains intact. In bee-eater nests, a hoe was used to create a vertical shaft to access the nest chamber from above. After accessing the nest, the top wall of the nest chamber was then rebuilt, and the access shaft filled in with soil.

The data used in this dissertation are begging call recordings of both honeyguide species and their primary hosts, all made at this field site, by Claire Spottiswoode (2008–2011), Luke McClean (2016–2018), Jess Lund (2021–2023) and myself (2022). In 2022, I also conducted a playback experiment at barbet nests, the methods and results of which are presented in Chapter 3.

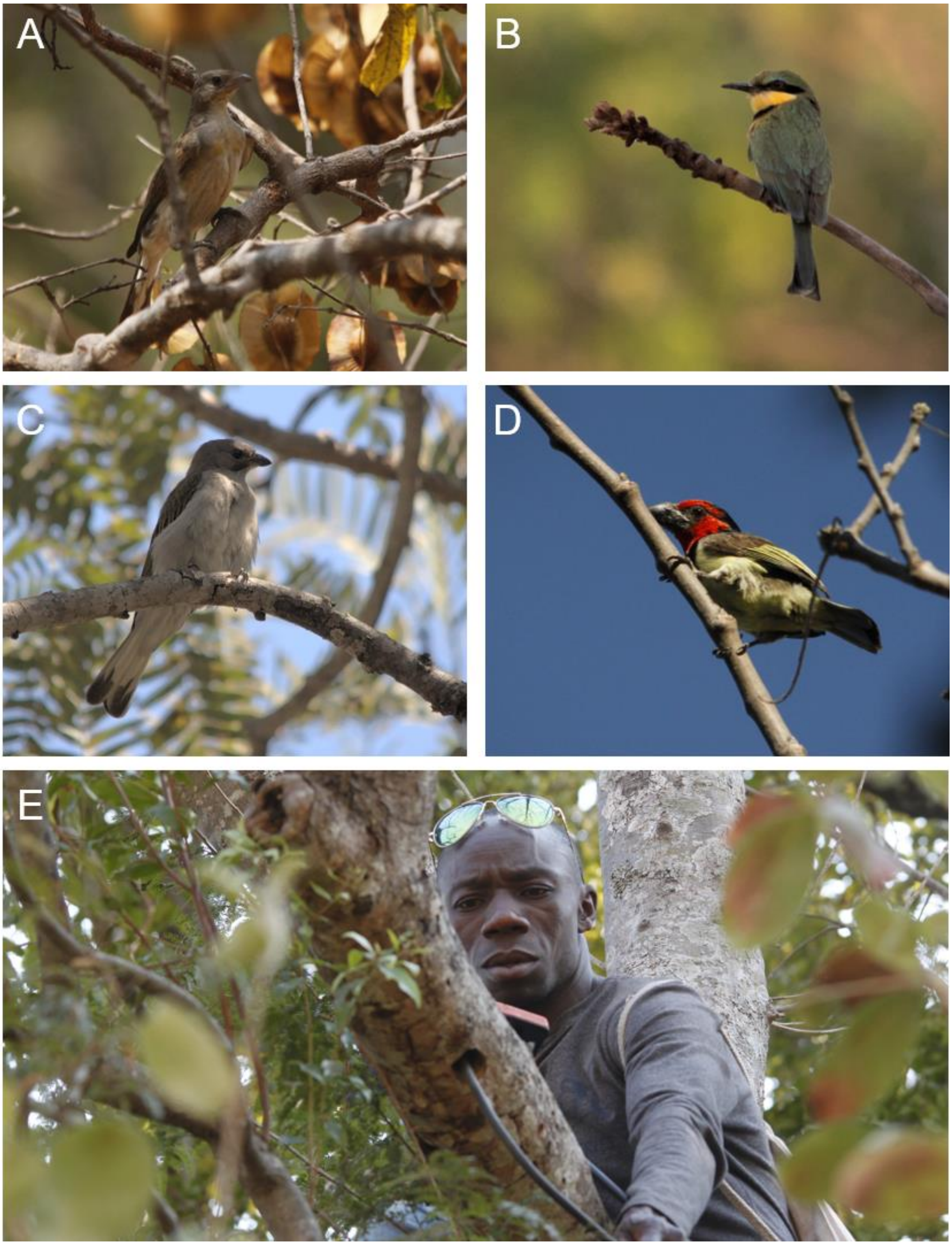
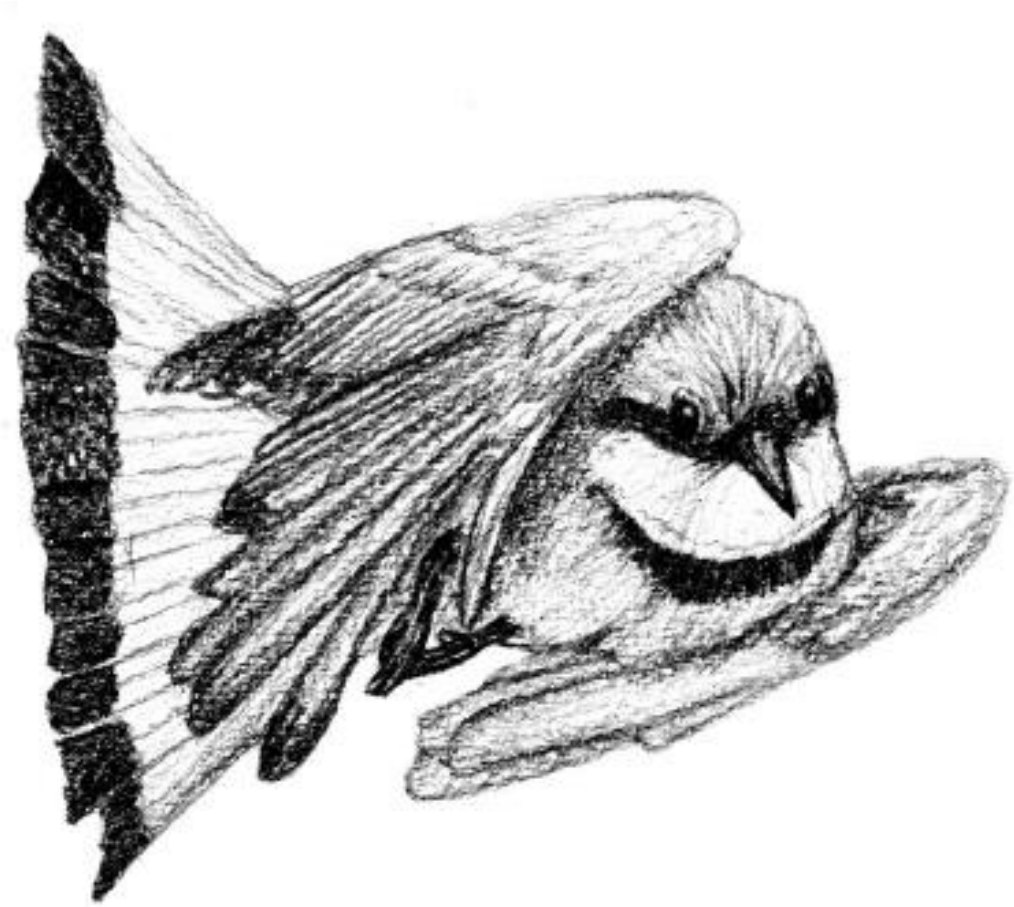


Figure 1.1: (A) Immature (formative plumage) greater honeyguide photographed at the field site. (B) Adult little bee-eater, the primary host of the greater honeyguide at the field site, carefully watching from a prominent perch near a nest burrow. (C) Lesser honeyguide near an active barbet nest, waiting for its opportunity to enter the nest and lay an egg. (D) Agitated adult black-collared barbet, the primary host of

lesser honeyguide at the field site, shortly after chasing an adult lesser honeyguide trying to enter its nest. (E) Primary field assistant Silky Hamama checking the status of a black-collared barbet nest using a Ridgid CA-25 endoscope. All photographs taken by Cameron Blair.

CHAPTER 2

Brood-parasitic honeyguide chicks mimic individual host chicks, not broods.



2.1 Abstract

The nestlings of brood-parasitic birds must avoid detection and secure sufficient food host parents, especially when their needs surpass those of the host nestlings. Nestling begging calls likely convey information about both identity and food requirements, providing brood-parasitic nestlings with a means to exploit communication channels between host parents and nestlings to obtain more food. Mimicry of host begging signals is widespread among brood parasites, yet many suspected cases lack quantitative investigation. Brood parasites often call at high rates to elicit supernormal provisioning from host parents, likely because high call rates sound to parents like multiple hungry nestlings. Greater (*Indicator indicator*) and lesser (*I. minor*) honeyguides are brood parasites of the little bee-eater (*Merops pusillus*) and black-collared barbet (*Lybius torquatus*) respectively. They are suspected to mimic their primary hosts' begging calls, and to mimic features of host broods to ensure they are fed at a high rate by host parents. This chapter examines evidence for primary host mimicry by honeyguides by comparing the similarity of their begging calls to those of their primary hosts, and between honeyguide species. I found that honeyguide calls more closely resembled those of their primary hosts than those of the other honeyguide species, supporting the mimicry hypothesis. I then tested whether honeyguides either match the call rate of host broods, and/or exploit any other features associated with multiple nestlings to enhance provisioning. I found no significant differences in trill or syllable rates between honeyguides and single nestlings of their respective hosts (perhaps because these are already near their upper physical limit), or in the other spectral and temporal features that differed between host single nestlings and host broods. These results imply that honeyguides mimic begging calls of their host species but not specifically features of host broods, suggesting that they must use some other mechanism to elicit high rates of parental provisioning.

2.2 Introduction

Brood-parasitic birds lay their eggs in the nests of other birds to avoid the costs of parental care. To be fed by their host parents, nestlings of brood parasites face two distinct challenges: (i) avoiding detection as parasites, and (ii) ensuring that they are fed enough food, since many brood parasites have different food requirements to the host nestlings (Jamie & Kilner 2017). Begging displays, which include begging calls (and, in some cases, postural displays) are widespread in birds with both altricial and precocial young (Johnstone & Godfray, 2001). These displays may provide a cue of nestling identity to parents so that parasites can be detected (Jamie & Kilner, 2017; Langmore, Hunt & Kilner, 2003), and also provide important signals to adult birds of how much food to provide to their nestlings (Budden & Wright, 2001; Johnstone & Godfray, 2001). Therefore, some brood-parasitic species appear to mimic host begging signals to evade detection and ensure adequate provisioning by host parents (Jamie & Kilner, 2017; Jamie et al., 2020).

Mimicry has evolved in many biological systems to prevent the accurate identification of an organism (Dalziell, Welbergen & Magrath, 2014; Vane-Wright, 1980). It can be used defensively to evade predation, or aggressively by predators and parasites to increase their success (Dalziell, Welbergen & Magrath, 2014). What constitutes mimicry has been debated (Vane-Wright, 1980; Dalziell, Welbergen & Magrath, 2014). A popular framework for defining avian vocal mimicry was developed by Dalziell, Welbergen & Magrath (2014), proposing that mimicry requires that (i) the signals of the mimic and the model resemble one another, (ii) the signal receiver changes its behaviour due to the resemblance in signals, and (iii) this behavioural change confers a selective advantage to the mimic (Dalziell, Welbergen & Magrath, 2014). Thus, resemblance between signals of brood parasites and host nestlings is not enough to demonstrate mimicry, since resemblance may also arise through convergent evolution due to identical nest environments, due to random matching leading to similarity as a result of chance, or through common ancestry (De Jager & Anderson, 2019; Grim, 2004; Jamie & Kilner, 2017). Convergent evolution due to similar nest environments is unlikely to be a widespread cause of host and parasite similarity. This is because selection pressures that are influenced by the nest environment, such as predation, are not sufficiently different between the nest environments of different hosts to explain the close matching between the begging calls of many brood parasites and their hosts (Jamie & Kilner, 2017). Similarly, random matching could account for some cases of similarity between brood parasites and their hosts (De Jager & Anderson, 2019), but similarity to host begging calls appears to be widespread in brood parasites and it is unlikely that most of these observed similarities are the result of chance (Jamie & Kilner, 2017). To assess which of the remaining mechanisms is likely responsible for resemblances between brood parasites and their hosts, features of brood parasite begging calls can be compared to those of both hosts and a close relative of the brood parasite. If ancestry predicts begging call structure, then brood parasite calls should resemble those of their own close relatives more than those of their hosts. Conversely, if selection from host parents has led to brood-parasitic mimicry, then brood parasite calls should resemble those of their hosts more than those of their close relatives.

The brood-parasitic honeyguides (Indicatoridae) provide a good system to explore whether the begging call structure of a brood parasite is shaped by ancestry or selection by host parents. At my study site in southern Zambia, two sympatric and closely-related brood parasite species, the greater (*Indicator indicator*) and lesser (*I. minor*) honeyguides, respectively parasitise little bee-eaters (*Merops pusillus*, hereafter “bee-eater”) and black-collared barbets (*Lybius torquatus*, hereafter “barbet”) as their primary hosts (McClean, 2020; Spottiswoode & Colebrook-Robjent, 2007; Spottiswoode et al., 2011). Working with two closely related sympatric brood parasites, which parasitise two distantly related hosts, allows us to compare the begging calls of each parasite with those of one another, as well as with those of their respective host. This allows us to infer whether each host species is imposing selection on the begging calls of parasite nestlings. Both primary hosts are hole-nestling birds, with barbets excavating holes in trees, and bee-eaters making tunnels in the ground. Since there is very poor light in their nests, any visual cues or signals such as posture or gape appearance are unlikely to be used by host parents, making acoustic signals and cues almost certainly the most important channel for parent-offspring communication. Thus, this system is ideal for specifically testing the effect of begging calls on host provisioning since there are negligible confounding effects of visual cues and signals.

Both honeyguide species are always raised alone in the nest, due to honeyguide hatchlings killing all host hatchlings by biting and shaking them using a pair of sharp hooks on the tip of their bill (Spottiswoode and Koorevaar, 2012). Greater and lesser honeyguide nestlings both need more food than the nestlings of their primary hosts, but for different reasons (McClean, 2020): greater honeyguides are much larger than little bee-eaters (approximately 50 g and 15 g respectively) and their nestlings grow at twice the rate of bee-eater nestlings. As a result, greater honeyguides need a higher rate of provisioning (McClean, 2020). By contrast, lesser honeyguides are smaller than barbets, but barbet parents feed honeyguide nestlings predominantly fruit, which they don’t digest well. Thus, honeyguide nestlings appear to need more food to offset this poor quality diet (McClean, 2020).

We know from playback experiments that begging calls of both honeyguide species elicit higher rates of parental provisioning than begging calls of single host chicks, and similar rates to begging calls of host broods (McClean 2020). However, the features of the honeyguide begging calls that elicit high provisioning rates are not yet known. Jubb (1966) first suggested that greater honeyguide nestlings may mimic a brood of host nestlings after hearing a greater honeyguide nestling in a green wood-hoopoe (*Phoeniculus purpureus*) nest, and Fry (1974) made a similar suggestion inspired by hearing greater honeyguides begging in the nests of red-throated bee-eaters (*Merops bulocki*). McClean (2020) concurred, since a playback experiment in both lesser and greater honeyguide hosts showed that begging call playback of honeyguide begging calls elicited a similar level of host provisioning to playback of host brood begging calls, which were both significantly higher than that elicited by begging calls of a single host nestling and a brood of an unrelated species (McClean, 2020).

One mechanism through which brood mimicry might be achieved is through high rates of calling. This is most likely to apply when hosts have a simple begging call structure and when host nestlings typically beg simultaneously, because in these cases call rate is proportional to the number of nestlings and so provides a useful cue to parents of the number of nestlings requiring food (Butchart et al., 2003). High call rates in brood parasites, often matching those of a host brood, have been shown in a few systems where the parasite's needs exceed those of individual host nestlings (Butchart et al., 2003; Davies, Kilner & Noble, 1998; Kilner, Noble & Davies., 1999; Madden & Davies, 2006). The best studied example is the common cuckoo (*Cuculus canorus*), a generalist brood parasite which is much larger than its hosts and so develops faster. Common cuckoo chicks evict host chicks from the nest and use a high rate of calling to make up for the deficient visual stimulus of a single gape (Davies, Kilner & Noble, 1998; Kilner, Noble & Davies., 1999). They adjust their rate of calling through experience to slightly exceed that of a brood of the host species, each of which has a simple begging call structure and broods that beg simultaneously (Butchart, 2003; Davies, Kilner & Noble, 1998; Kilner, Noble & Davies, 1999; Madden & Davies, 2006). Common cuckoo nestlings adjust their begging call rate to different host species, because each species responds differently to call rate depending on the signals provided by their own young, and so the optimal call rate to ensure optimal provisioning differs between hosts (Butchart et al., 2003). However, the structure of individual call elements in the cuckoo's begging calls appear similar in the nests of different host species, suggesting that call rate is the only feature of common cuckoo begging calls that is adjusted between different hosts (Butchart et al., 2003). In non-evicting brood parasites where the parasitic chick is raised alongside host chicks, the challenge is different since non-evicting brood parasites need to compete with host nestlings for access to food. Such parasites can use high call rates to both increase overall rates of provisioning to the brood and access a higher proportion of the food provisioned (Boncoraglio, Saino & Garamszegi, 2009; Gloag & Kacelnik, 2013; Ursino et al., 2018). For example, shiny cowbird (*Moluthrus bonariensis*) chicks do not evict host chicks and parasitise a wide range of host species that have begging calls with a simple structure. Shiny cowbird nestlings produce rapid, tremulous calls that appear to mimic the sound of multiple nestlings in general, rather than mimicking specific hosts (Gloag & Kacelnik, 2013). The tremulous calls of the shiny cowbirds also increased provisioning rates of great tits (*Parus major*), which are naïve to parasitism and distantly related to cowbird hosts, suggesting that such a response to high call rate is likely conserved across birds (Gloag & Kacelnik, 2013).

Taken together, these results indicate that a high call rate is an effective mechanism that brood-parasitic nestlings can use to increase provisioning across a wide range of host species which have simple begging call structures (Gloag & Kacelnik, 2013). This effect may arise because high call rates either (i) create the perception in the host parent that there are more nestlings than they actually are (brood mimicry), or (ii) exploit a more general sensory bias in the host parent through a supernormal stimulus. Brood mimicry is likely to be an effective parasitic strategy when call rate is a cue that host parents use to assess the number of nestlings that need feeding. By contrast, supernormal stimulus could be an effective parasitic strategy when call rate is not a useful cue to the number of nestlings (such as when nestlings do not beg simultaneously), but when host parents nonetheless still have a sensory bias towards higher call rates, such that they have an elevated response to call rates exceeding those of their own nestlings (Gloag & Kacelnik, 2013; Kilner, Noble & Davies., 1999). If it is the result of a sensory bias, this bias may develop if higher call rates are signals of that nestlings need to be provided more food.

Although call rate is the only acoustic mechanism that has so far been demonstrated to increase provisioning (Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2013; Kilner, Noble & Davies., 1999, Rojas Ripari et al., 2021), parasites could also use both brood mimicry and supernormal exaggeration of features associated with nestling need to exploit host vulnerability with respect to other acoustic features of host broods. First, parasites could use brood mimicry of features besides call rate if these also depend on the number of nestlings present. I suggest that the disorder of the acoustic energy in both frequency and time domains may provide one such possible cue of brood size that could be vulnerable to parasitic exploitation. To illustrate this, consider a single nestling begging. Each syllable occurs for a distinct amount of time with regular periods of silence between syllables, and at a regular pitch and harmonic structure. However, if multiple nestlings beg simultaneously, the result is much more chaotic and the organisation of the acoustic energy through time is more random, without the discrete periods of silence and sound. Additionally, it is likely that each nestling has slightly different pitched calls, such that the interference between the calls of nestlings adds further chaos to the frequency spectrum at each point in time. Moreover, even if nestlings do not beg simultaneously, competition with other nestlings in the brood may also lead to differences in the begging call structure of individual nestlings in a brood or alone. For example, if there are multiple nestmates, individual nestlings face more competition for food, and are more likely to dishonestly signal that they need more food than they actually require (Caro, West & Griffin, 2016). Thus, the structure of the begging calls of individual nestlings may influence parental provisioning rate, and brood parasites may benefit from mimicking these features. In other words, parasites could mimic a brood not by sounding like a brood, but by sounding like an individual within a brood.

Second, parasites could use supernormal stimulus of features besides call rate if there are begging call features that host parents associate with nestling hunger (rather than number of nestlings), which brood parasites could exaggerate to increase host provisioning to levels higher than they typically provide to broods of their own. This is a plausible hypothesis since several features of begging calls have been demonstrated to be associated with nestling hunger in non-parasitic species, including peak frequency and frequency range (Anderson, 2010; Sacchi et al., 2002), amplitude (Anderson, 2010; Corney & Barber, 2018), and the duration of call syllables (Anderson, 2010; Sacchi et al., 2002). These therefore provide candidate mechanisms which brood parasites could exploit to manipulate provisioning by host parents to supernormal levels. However, in theory, the upper limit of an exaggerated feature may be constrained if excessively exaggerated features become a reliable cue that host parents can use to detect parasitism or cease to be recognisable such that host parents stop responding to it (Holen et al., 2001). The possibility of parasites producing a supernormal stimulus through mechanisms besides brood mimicry has yet to be investigated empirically, however, except in cases where “begging intensity” has been subjectively assessed (Bolopo et al., 2015; Bortolato et al., 2019; Lichtenstein, 2001; Rivers 2007; Rivers et al., 2010).

In brood parasites that parasitise multiple host species, however, mimicking general features of host broods or using a supernormal stimulus may not be enough to increase provisioning in every instance, since species-specific mimicry of certain features of host begging calls can also be necessary to ensure enough provisioning. For example, baywings (*Agelaioides* spp.) are parasitised by the specialist screaming cowbird (*Moluthrus rufoaxillaris*), which has a similar call structure to baywing nestlings (Ursino et al., 2018). Provisioning by greyish baywings (*A. badius*) was higher to nestlings of screaming cowbirds (and similar to provisioning of single host nestlings), than to nestlings of shiny cowbirds, a generalist brood parasite whose rapid, tremulous begging calls are not adapted for a specific host (Ursino et al., 2018). Thus, brood mimicry or a supernormal stimulus may be insufficient on their own to elicit higher rates of provisioning to brood parasites in all instances. Species-specific mimicry may also be required so that the host parents first recognise the begging call as one that resembles their own nestlings, before possible mechanism to manipulate host provisioning is effective.

In this chapter, I tested whether the potential mechanisms mentioned above may explain how honeyguides are able to use their begging calls to get fed more than the nestlings of their hosts. First, I tested whether there is evidence for begging call mimicry of their primary hosts by greater and lesser honeyguides and if so, with respect to which acoustic features. The hypothesis that honeyguides mimic the begging calls of their primary hosts predicts that each honeyguide species will have begging calls that are more similar to those of their host than to those of the other honeyguide species. By contrast, if the begging calls of each honeyguide species resemble those of one another more than those of their primary host, then honeyguides likely do not mimic their primary hosts and the structure of their begging calls is better explained by phylogenetic descent.

Next, I asked how honeyguide nestlings achieve a higher rate of provisioning than individual host nestlings. I assessed whether there is evidence that honeyguides increase provisioning using (i) brood mimicry or (ii) supernormal stimulus of either call rate or other structural features of begging calls. I did so by comparing call rate (both syllable rate and trill rate) and other acoustic variables between honeyguides, host broods and single host nestlings. The hypothesis that honeyguides mimic a host brood, either in call rate or other structural variables, predicts that honeyguide begging calls should be more similar to host begging calls recorded when multiple chicks were present in the nest, compared to host begging calls recorded when just a single chick was present in the nest. Alternatively (although not mutually exclusively), honeyguides may use a supernormal stimulus that is independent of mimicking a host brood, and this hypothesis would predict that measurements of acoustic variables in honeyguide begging calls significantly exceed those of either a host brood or single host nestling.

Taken together, these analyses answer whether honeyguides mimic their primary host, and whether the observed high provisioning rates by their primary hosts are due to honeyguides mimicking a host brood or producing supernormal stimuli (provided by either call rate or other structural features).

2.3 Methods

2.3.1 Collection of begging call recordings

Recordings analysed in this study were made by Claire Spottiswoode (2008–2011), Luke McClean (2016–2018), Jess Lund (2021–2023) and myself (2022). All recordings were made by placing an omnidirectional lapel microphone (Audio-Technica ATR-35S or ATR-3350, Audio-Technica, Shinjuku, Japan) into the nest chamber of barbets and bee-eaters in a manner that did not disturb the host parents. For details of how barbet and bee-eater nests were accessed, see Section 1.6. At barbet nests, the thin cable of the lapel microphone led through the space between the door and the surrounding wood. To reduce visibility, the cable was wrapped around the branch and the attached recorder was hidden using a piece of bark. In bee-eater nests, the lapel microphone was placed in the nest, with the recorder, housed in a plastic box, either being placed above ground and insulated and concealed with leaves or sand (in which case the microphone cable extended through a narrow plastic pipe to the recorder box), or being placed directly above the nest chamber. The top wall of the nest chamber was then rebuilt around the plastic pipe or plastic box, and the access shaft filled in with soil.

To make recordings with only a single chick in the nest, all except one nestling was removed from the nest, placed temporarily in an artificial nest made from a container lined with leaves and grass, and kept in the shade for a period of one hour. While the nestlings were not in the nest, they were closely monitored for any signs of distress (which none of them displayed).

Recordings were made in 16-bit or 32-bit WAV format to ensure that there was no loss of information (Araya-Salas, Smith-Vidaurre & Webster, 2019), with a sampling rate of 48 or 44.1 kHz using Sony Minidisc MZ-RH1 (Sony Corporation, Tokyo, Japan; 2008–2011) and Tascam DR-05 or DR-05X (TEAC Corporation, Los Angeles, USA; 2016–2023) digital audio recorders.

2.3.2 Development of begging calls and assignment of developmental stages

In both honeyguide species and their hosts, I identified three developmental stages by listening to begging call recordings. Newly hatched chicks have single syllable “peep” calls (stage 1), which develop into an intermediate stage where the calls start to develop more structure and become multisyllabic (stage 2). After this stage, they develop into a continuous “rolling” call which is very rapid (stage 3). Calls were assigned to one of these stages by ear. Some of the recordings had data on the mass of the nestlings when the recording was made. To assess whether these stages indeed corresponded to different ages or masses of chicks, I compared the distribution of masses in each stage as determined by ear and found that masses at different stages were broadly non-overlapping (Figure 2.2). This supports the classification of begging calls into these stages based on assessment by ear. Mass data were not available for stage 2 begging calls of barbets and lesser honeyguides, although there were recordings made of begging calls that appeared intermediate between stage 1 and stage 3 calls. Only stage 3 recordings were used for analyses, since these are the most complex calls and also were the ones used by McClean (2020) in his experiments.

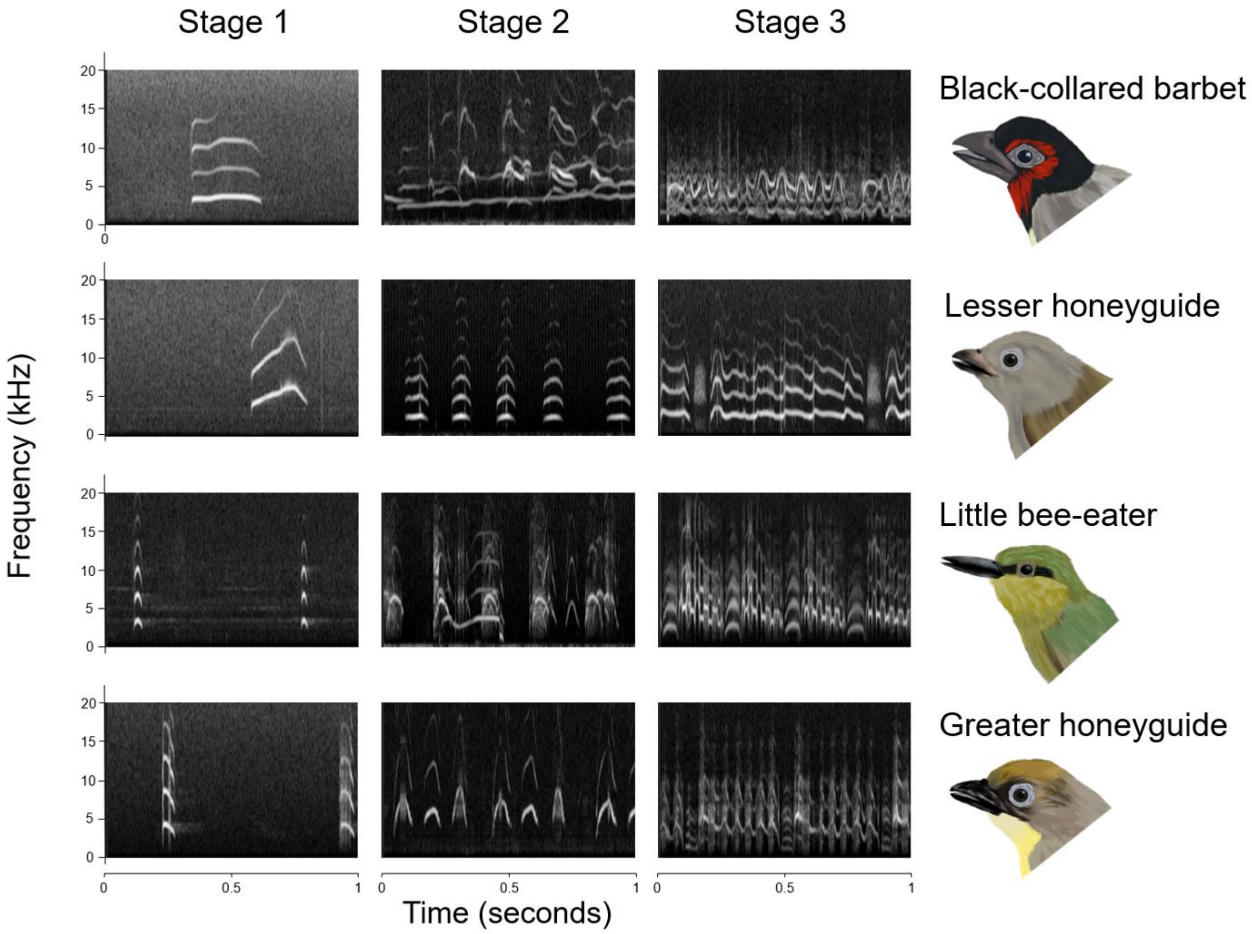


Figure 2.1: Spectrograms of each study species' begging calls at each stage. Stage 1 calls are given in the days after hatching, stage 2 is an intermediate stage where the calls develop more structure, and stage 3 is the final stage, which is a rolling call with trilled syllables.

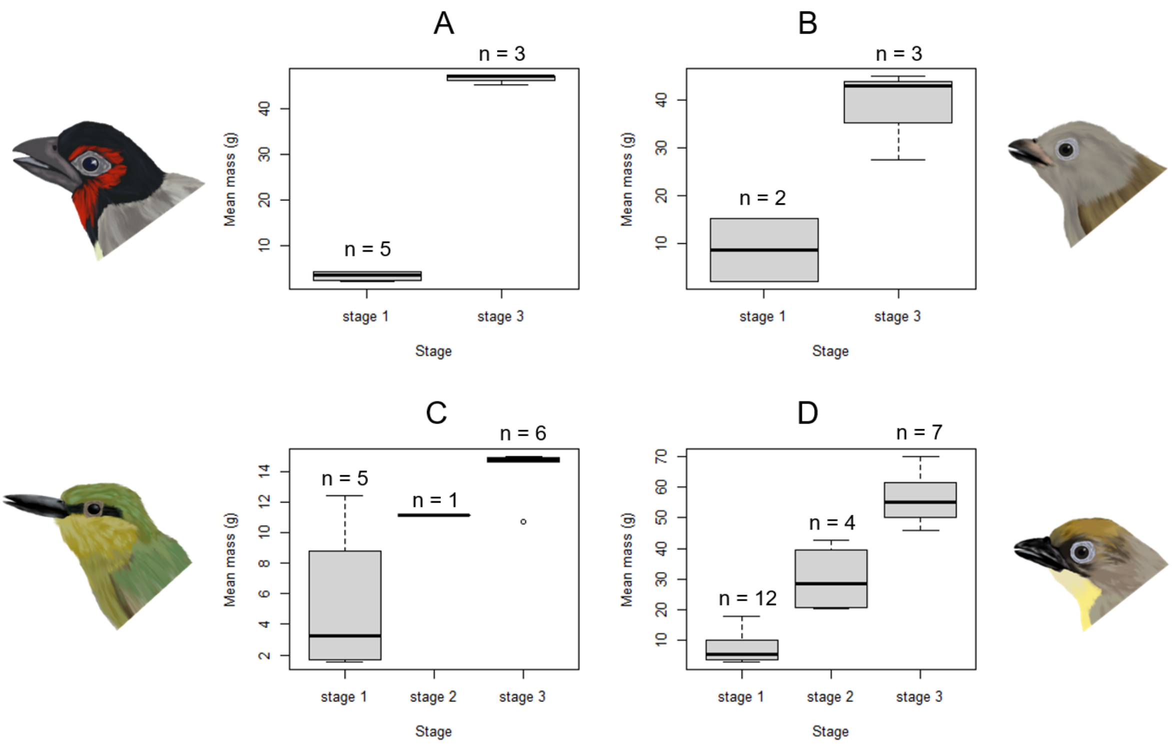


Figure 2.2: Developmental stages assigned to chicks by ear based on their begging calls correlated with mean nestling mass for each study species (A – black-collared barbet, B – lesser honeyguide, C – little bee-eater, D – greater honeyguide). Masses were only available for stage 1 and stage 3 black-collared barbets and lesser honeyguides. Note the difference in scale on the Y axis for little bee-eaters vs greater honeyguides since the latter are much larger than the former.

2.3.3 Recording preparation

Distinct bouts of nestling begging were typically triggered by the arrival of a host parent, and each recording contained between 1 and 19 such bouts. From each recording, I extracted a 5-s clip from the beginning of each begging bout. The beginning of a begging bout was identified by visually inspecting the waveform of each recording. I applied a high pass filter at 700 Hz cutoff frequency with a 24 dB roll off to each clip. I decided to use this cutoff level by examining spectrograms of each clip to determine the lower limits of pitch across recordings, which indicated that a threshold of 700 Hz resulted in no loss of information. I normalised the maximum amplitude of each clip to -3 dB to ensure recordings were at comparable amplitudes before analysis. Each of these processing methods were implemented using the software Audacity 3.2 (Muse Group, Limasol, Cyprus).

2.3.4 Trill and syllable rate measurements

In both honeyguide species and both their hosts, one syllable type present in all stage 3 begging calls was a trill made from varying numbers of elements repeated in quick succession (Figures 2.3 & 2.4). The rate of trilling for these syllables was assessed by taking 1-s clips from the beginning of each 5-s clip. The 1-s clips were then visualised using spectrograms in Raven Pro 1.6.5 (www.ravensoundsoftware.com), and the number of elements in the first complete trill syllable in each clip was counted and the duration of the syllable was measured. Trill rate was then calculated by dividing the number of elements in the trill syllable by its duration. Syllable rate was similarly measured by visualising spectrograms of the 5-s clips and counting the number of complete syllables in each clip. Since each clip was of the same length, the syllable count in each clip was a measure of syllable rate. Bee-eater nestlings did not typically call simultaneously, whereas barbet nestlings did. Thus, trill and syllable rates of broods could only be accurately counted in bee-eaters, and barbet brood recordings were excluded from trill and syllable rate analyses.

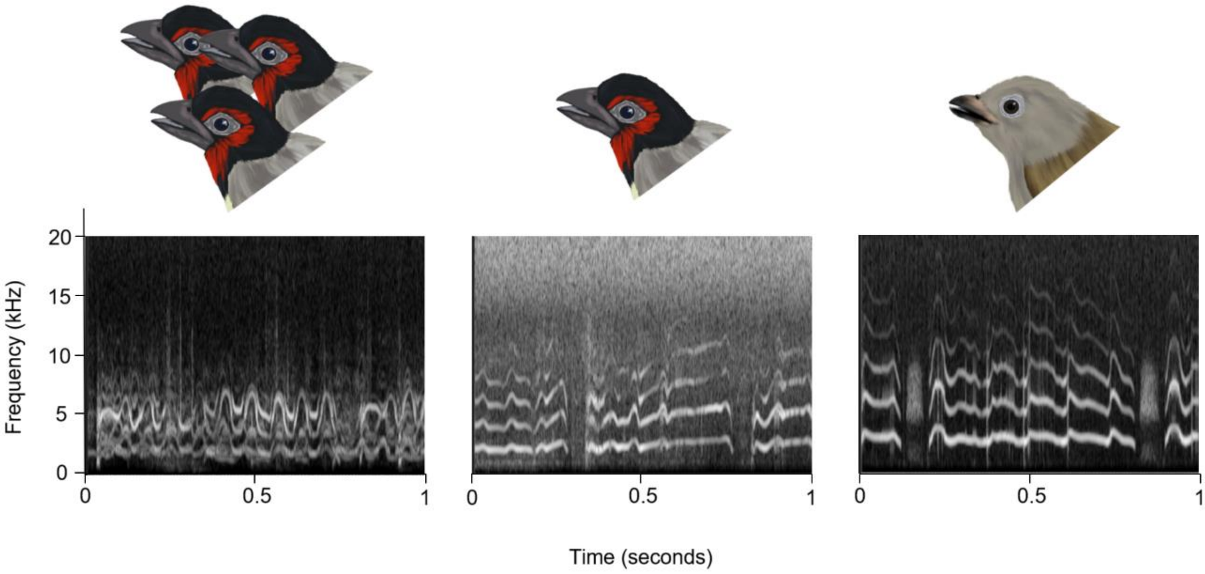


Figure 2.3: Spectrograms of stage 3 begging calls of (a) a black-collared barbet brood with nestlings begging simultaneously, (b) a single, black-collared barbet nestling, and (c) a single lesser honeyguide nestling.

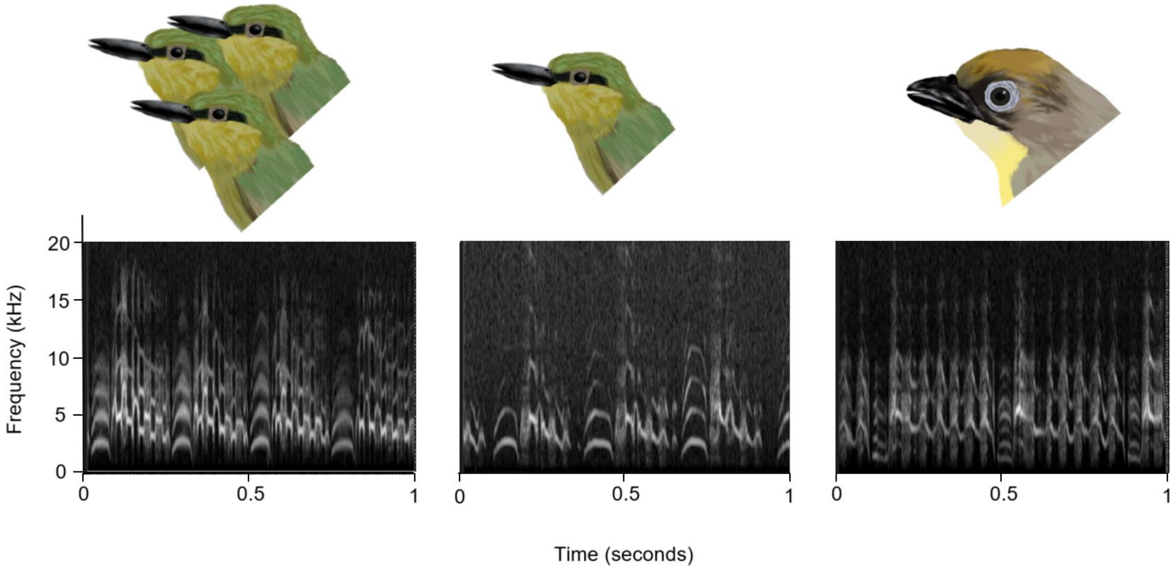


Figure 2.4: Spectrograms of stage 3 begging calls of (a) a little bee-eater brood with only a single nestling begging, (b) a single little bee-eater nestling, and (c) a single greater honeyguide nestling.

2.3.5 Statistical analysis

I conducted statistical analyses using R (R Core Team, 2023). I used the function *spectro_analysis* in package *warbleR* (Araya-Salas and Smith-Vidaurre, 2017) to extract measurements of many different acoustic parameters from each sound clip. I then chose the following parameters to use in the analyses: median frequency, median time, skewness, spectral entropy, time entropy, mean dominant frequency, dominant frequency range, modulation index, peak frequency and mean fundamental frequency (See Table 2.1 for their definitions). I chose these parameters from the larger set of parameters measured by *spectro_analysis* by grouping parameters that measure similar features of the sound structure. For example, possible measures of dominant frequency that can be measured by *spectro_analysis* are mean dominant frequency, maximum dominant frequency, minimum dominant frequency, start dominant frequency and end dominant frequency. From these groupings, one measurement was chosen that was considered the best for describing that feature for the purpose of the analyses. Measures of central tendency were chosen rather that measures of extremes, and median was chosen rather than mean, if available, since the median is more robust to outlying values, and represents a direct measurement rather than an estimated theoretical value (Rousseeuw, 1991). In the above example, mean dominant frequency was thus chosen from the options since it is a measure of central tendency and median was not available in the output from the function *spectro_analysis*. Reducing the number of variables tested was done to reduce the risk of false positives due to multiple testing.

Table 2.1: Variables extracted from clips of begging calls in each species, and their definition, taken from the documentation for the *warbleR* package (Araya-Salas & Smith-Vidaurre, 2017).

Variable	**Definition**
Median frequency	The frequency at which the frequency spectrum is divided in two frequency intervals of 25% and 75% energy respectively
Median time	The time at which the time envelope is divided in two time intervals of equal energy
Skewness	Asymmetry of the frequency spectrum
Spectral entropy	Energy distribution of the frequency spectrum
Time entropy	Energy distribution on the time envelope
Mean dominant frequency	Mean of dominant frequency measured across the spectrogram
Dominant frequency range	Range of dominant frequency measured across the spectrogram
Modulation index	Cumulative absolute difference between adjacent measurements of dominant frequencies divided by the dominant frequency range
Peak frequency	Frequency with the highest energy
Mean fundamental frequency	Mean fundamental frequency measured across the acoustic signal

2.3.6.1 Primary host mimicry

I took three complementary approaches to assess whether the two honeyguides were more similar to each other or to their primary hosts: (i) principal component analysis (PCA) to assess how begging calls differed with respect to a synthesis of the variables in Table 2.1, and which of these acoustic variables explained the most variation between species; (ii) dynamic time-warping (DTW) of the dominant frequency contours to determine which calls were the most similar to each other with respect to this specific feature, and how their frequency changes through the course of the begging call; and (iii) discriminant function analysis (DFA) and multinomial logistic regression (MLR) classification models to determine whether begging calls from each honeyguide species were classified more often as their host or as the other honeyguide species.

For the PCA, I used the *prcomp* function in *stats* (R Core Team, 2023). This method creates variables (principal components) from the measurements extracted which capture the maximum amount of the variation in the data and allow assessment of which acoustic variables explain the most variation, by examining their relative loadings. I assessed the differences between clips by visualising the first two principal components in a biplot created using *ggbiplot* (Vu, 2011). I then ran pairs of linear mixed-effects models (LMMs) using *lmer* in *lme4* (Bates et al., 2015) with the first principal component as the response, since this principal component explains the most variance. Species identity was included as a fixed factor in one of the models but not the other, to test for species differences, and nest identity was included as a random effect in all models to avoid pseudoreplication from multiple recordings of the same nest. To avoid pseudoreplication introduced by analysing multiple clips from the same recording, I resampled one clip from each recording for 100 iterations of model pairs and obtained 100 sets of results, from which I could calculate the percentage of iterations for which a particular test was significant. I took this approach rather than including the recording identity in the random effects structure of the LMMs, since inclusion of a nested random effect structure led to singular model fit. I assessed homoscedasticity and normality of the residuals using residual and quantile-quantile plots created using *mcp.fnc* in *LMERConvenienceFunctions* (Tremblay and Ransijn, 2020). I assessed the effect of species identity on the response using model comparison based on corrected Akaike's Information Criteria (AICc) between the two models with the *AICc* function in *MuMIn* (Bartoń, 2022). I conducted post-hoc comparisons between the species by calculating the estimated marginal means and their confidence intervals using the *emmeans* function from the *emmeans* package (Lenth, 2023). I conducted Tukey's Significance Tests using the *pairs* function in *emmeans* (Lenth, 2023) for the pairwise comparisons between each honeyguide and their primary host, as well as between the two honeyguide species.

For the DTW analysis, I extracted DTW distances between clips using the function *freq_DTW* from the *warbleR* package (Araya-Salas and Smith-Vidaurre, 2017). This method calculates the cross-correlation in dominant frequencies between clips throughout the length of a recording, while warping the time axis to achieve the highest cross-correlation between clips. Therefore, slight differences in the speed or alignment of two calls does not affect the distance measurement. Instead, it is the dominant frequencies and their patterns of change through time that are compared independent of their speed. DTW of frequency contours has been recommended for assessing similarity in begging calls of brood parasites and their hosts when the perceptually salient features are not known (Ranjard et al., 2010). Similarly to the PCA, I assessed the similarity between the honeyguides and each of their hosts, as well as between the two honeyguides, to test for evidence for mimicry. I did this by examining the DTW distances between them. I visualised the DTW distances between clips by conducting classical multidimensional scaling (MDS) into two dimensions using the function *cmdscale* in the *stats* package (R Core Team, 2023) and plotting the eigenvalues using *ggplot2* (Wickham, 2016). I performed permutation tests to statistically compare the DTW distances between each honeyguide and their primary hosts, as well as between the two honeyguides. For each comparison, I calculated the mean DTW distance between species. Recordings were then randomly assigned a “species” label, regardless of their true species, and the distance between the same two species was calculated. This process was repeated 1000 times and a *p*-value calculated by determining what proportion of the calculated distances with randomised labels was less than the observed mean distance between the two species.

For the DFA and MLR classification models, I ran two models of each type: one trained on lesser honeyguide and little bee-eater data, which was used to classify greater honeyguide begging calls, and another trained on greater honeyguide and black-collared barbet data, which was used to classify lesser honeyguide begging calls. This assesses whether honeyguide begging calls were more likely to be classified as another honeyguide species or as their primary host. If honeyguide calls are consistently classified as their host, then there is evidence for mimicry. However, if they are classified as another honeyguide, then begging call structure is explained better by common ancestry. Both classification models tested similar questions, but MLR makes fewer assumptions, whereas DFA performs better with smaller sample sizes (Pohar et al., 2004, Jamie et al., 2020). I therefore decided to conduct both and compare results for robustness. I conducted the DFA using the *lda* function in the *MASS* package (Venables and Ripley, 2002), and conducted the MLR using *multinom* in the package *nnet* (Venables and Ripley, 2002).

2.3.6.2 Is there evidence for brood mimicry or supernormal stimulus in call rate?

I used generalised linear mixed-effects models (GLMMs) to compare trill and syllable rates between each honeyguide species and its host. I used planned contrasts rather than post-hoc pairwise comparisons between all groups to increase statistical power, since not all pairwise comparisons are of interest (Ruxton & Beauchamp, 2008; Schad & Kliegl, 2020). In greater honeyguides and bee-eaters, I included the following planned contrasts in the models: (i) bee-eater brood vs single bee-eater nestling, and (ii) greater honeyguide vs little bee-eater brood. In lesser honeyguides and barbets, there were no planned contrasts between the categories since there were only two categories (lesser honeyguides and single barbet nestlings) because barbet nestlings beg simultaneously (see section 2.3.4).

I calculated trill rate by dividing the number of elements in the trill syllable by the duration of the measured syllable. Since these values were not integers, were positive, and had a positively skewed distribution, I used a gamma distribution for the GLMMs with a log link-function (Zuur et al., 2012). Since I recorded syllable rate as a count within the 5-s clip, I was able to use a Poisson distribution for the models with syllable rate as the response (Zuur et al., 2012). I also used a log link-function for these models. I implemented the gamma GLMMs using the *glmmTMB* function in the *glmmTMB* package (Brooks, 2017) and the Poisson GLMMs were implemented using *glmer* in the *lme4* package (Bates et al., 2015).

2.3.6.3 Is there evidence for mimicry or supernormal stimulus in other structural features?

Next I tested whether (and if so, what) acoustic differences existed between the structure of begging calls produced by a whole brood of host nestlings compared to a single host nestling, then tested whether honeyguides differed from their hosts in these same features. To do so, I first conducted both DFA and MLR using leave-one-out cross validation. The DFA and MLR were implemented using the functions *lda* from the *MASS* package (Venables and Ripley, 2002) and *multinom* from the *nnet* package (Venables and Ripley, 2002), respectively. I calculated the accuracy of leave-one-out cross-validation predictions to assess the classifying performance of the models. I assessed the most useful features to differentiate between recordings of host broods and single nestlings by examining the coefficients of the first linear discriminant function in the DFA. Variables that had absolute values higher than 1 for their associated coefficients were considered as more useful to distinguish between host broods and single nestlings. For the MLR, I used analysis of deviance with type III sums of squares to assess which variables were better predictors of whether a begging call came from a host brood or single nestling. I conducted the analysis of deviance using the *aov* function in the *stats* package (R Core Team, 2023). Variables with a *p*-value less than 0.15 were considered as the most useful for to distinguish between host broods and single nestlings. This threshold was chosen instead of the more common 0.05 threshold so that at least two variables were below the threshold for each system (see Section 2.4.2.2).

Next, I compared the begging calls of honeyguides to single host nestlings and host broods, to assess whether honeyguides differ from single nestlings in a similar manner to host broods. I conducted pairs of LMMs with the variables from each classification model type that were the best predictors of whether a clip is from a host brood or single nestling as the response, since each of these is a candidate feature of the begging call that is hypothesised to provide a cue to the host parents of how many nestlings are in the nest. In each pair of LMMs, I included the category of the clip (honeyguide, single host nestling, host brood) as a fixed factor in one of the models but not the other. Recording identity was nested within nest identity as a random factor in each model, except in cases where the model had a singular fit or did not converge. In these cases, I ran 100 iterations of model pairs with one random clip taken from each recording per iteration, and recording identity dropped from the random effects structure. I implemented the LMMs using *lmer* in the *lme4* package (Bates et al., 2015) and tested assumptions using *mcp.fnc* in *LMERConvenienceFunctions* (Tremblay and Ransijn, 2020). I used AICc-based model selection using the function *AICc* in *MuMIn* (Bartoń, 2022) to assess whether there was a difference between the categories in the selected variables. I conducted Tukey's Significance Tests to assess the pairwise differences between each of the categories using *pairs* in the *emmeans* package (Lenth, 2023).

2.4 Results

I analysed 532 clips, taken from the beginning of each begging bout in 129 stage 3 recordings from 83 nests. These were collected from 31 unparasitised black-collared barbet broods (32 full brood recordings, comprising 2–4 chicks, and 9 recordings of single nestlings), 12 single lesser honeyguide chicks in black-collared barbet nests (13 recordings), 20 unparasitised little bee-eater broods (15 full brood recordings, comprising 2–5 chicks, and 10 recordings of single nestlings), and 20 single greater honeyguide chicks in little bee-eater nests (50 recordings).

2.4.1 Do honeyguides mimic their primary hosts?

2.4.1.1 Principal components analysis

I conducted principal component analysis (PCA) to assess the similarity between clips by taking multiple measurements of begging call structure and reducing them into principal components that retained the most variation in the original data. Visualisation of the two principal components that explain the most variation (PC1: 33.9% explained variance; PC2: 18.8% explained variance) in a biplot showed a clear pattern whereby each honeyguide species showed greater overlap with its respective hosts than with the other honeyguide species (Figure 2.5).

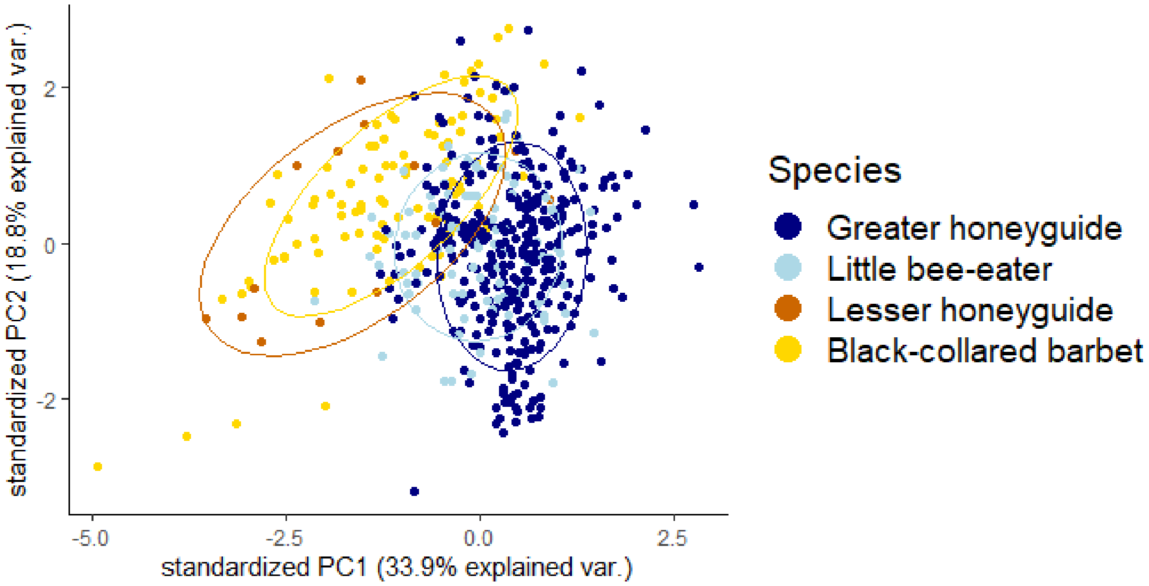


Figure 2.5: Biplot of the two principal components that explained the most variance from the principal components analysis. Individual dots represent each 5-s begging call clip. Normal data ellipses (69%) are drawn for each species. See main text for statistical analyses taking into account non-independence of clips from the same individual.

Table 2.2: Loadings of the first two principal components (PC1 and PC2) on the acoustic variables.

Variable	PC1	PC2
Frequency median	-0.244	-0.701
Time median	-0.184	-0.003
Skewness	0.339	0.016
Spectral entropy	0.451	0.239
Time entropy	-0.009	-0.008
Mean dominant frequency	-0.388	0.667
Dominant frequency range	-0.063	-0.061
Modulation index	-0.010	0.013
Mean peak frequency	0.659	-0.045

To determine whether the differences between species in PC1 were significant, while taking into account non-independence of clips from the same individuals, I ran 100 iterations of LMM pairs (see Section 2.3.6.1). In every iteration, the LMM with species identity was significantly better fitting than the model with species identity excluded (ΔAICc > 2), suggesting that there are differences in PC1 between at least two species. The distribution of estimated marginal means for each species from the models confirmed that each honeyguide species was more similar to their hosts than to each other (Figure 2.6A). Tukey's honest significance tests on the estimated marginal means supported this, showing that in the majority of iterations, the difference between each honeyguide and its primary host was non-significant (Figure 2.6B), whereas the majority of iterations (75/100) showed a significant difference between the two honeyguides (Figure 2.6B). The median frequency, mean dominant frequency and mean peak frequency contributed the most to the first principal component, based on their loadings (Table 2.2). Taken together, these results suggest that honeyguides mimic their hosts' begging calls, and specifically their frequency.

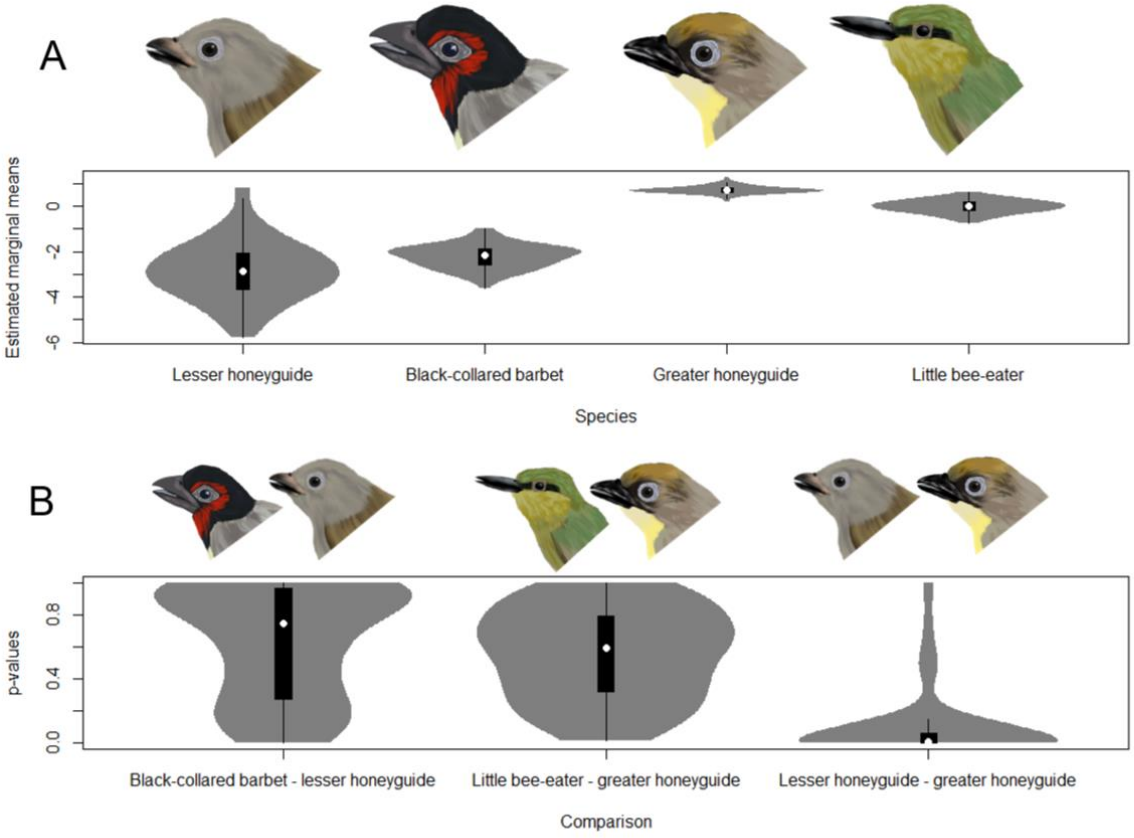


Figure 2.6: Greater and lesser honeyguides are more similar to their primary hosts than they are to each other, in the first principal component (PC1) summarising acoustic variation in begging calls. Violin plots show the distribution (based on 100 resamples to avoid pseudoreplication within individuals) of (a) marginal means of PC1 for each species, estimated from each linear mixed-effect model, and (b) adjusted *p*-values from Tukey's honest significance tests for the pairwise comparisons between each honeyguide and their primary host, as well as between the two honeyguides.

2.4.1.2 Dynamic time-warping distances

In addition to the PCA, I conducted a similarity analysis using dynamic time-warping (DTW) of the dominant frequency contours. This provides a dissimilarity (distance) metric between pairs of clips.

Visualisation of the DTW distances using multidimensional scaling into two dimensions (Figure 2.7) suggests that begging call clips from host-parasite pairs are the most similar to each other, and honeyguides are the least similar to each other. However, the 95% normal data ellipses of each species overlap with each other, indicating that this pattern is not shown across all clips.

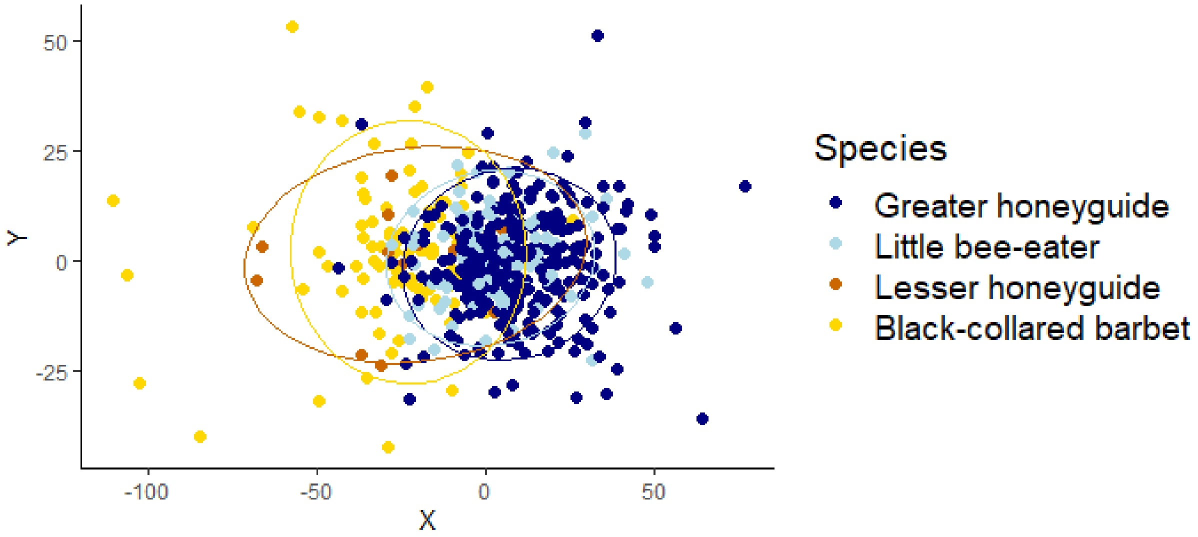


Figure 2.7: Multidimensional scaling plot showing the best representation of the relative dynamic time-warping distances between each clip possible in two dimensions. Each dot represents a begging call clip, and colours indicate species. 95% normal data ellipses are drawn for each species.

The distribution of DTW distances for each species shows that distances between clips were on average greater between the two honeyguide species than between the honeyguides and their respective primary host species. However, there was much overlap (Figure 2.8A) and permutation tests did not find any evidence in any of the comparisons that the distance between the two groups is any less than would be expected by chance (permutation tests, Figure 2.8B).

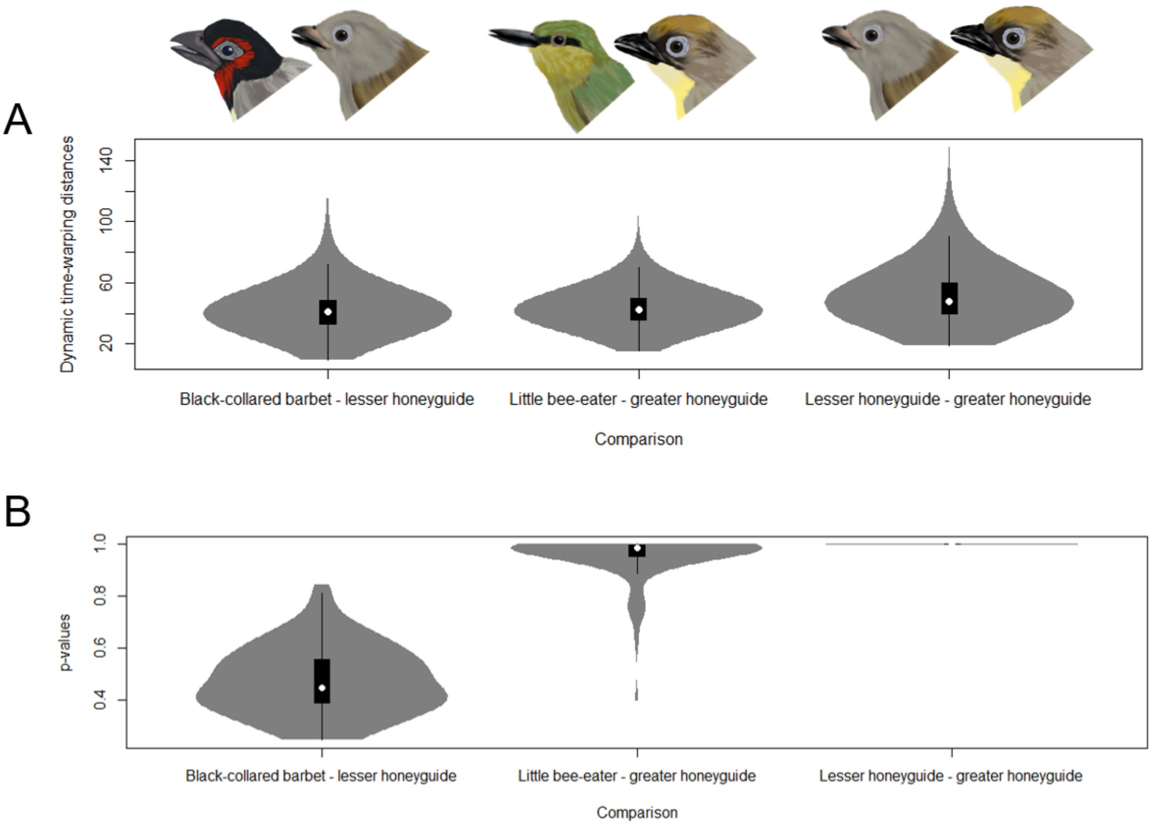


Figure 2.8: Dynamic time-warping (DTW) distance between host-parasite pairs are not significantly closer than that between honeyguides species. Violin plots showing (a) the distribution of dynamic time-warping distances for each of the species comparisons, and (b) the distribution of *p*-values. Distances and *p*-values result from 100 permutation tests with one random clip taken from each nest for each iteration, and the dynamic time-warping distances calculated. The following comparisons were made: black-collared barbet vs lesser honeyguide, little bee-eater vs greater honeyguide, and lesser vs greater honeyguide.

2.4.1.3 Classification models

To determine whether honeyguide begging calls are consistently classified by a model as their host or as the other honeyguide species, both DFA and MLR models were run(?) (details in Section 2.3.6.1). For each type, I ran two models: (i) greater honeyguide recordings classified by a model trained on lesser honeyguide and little bee-eater recordings, and (ii) lesser honeyguide recordings classified by a model trained on greater honeyguide and black-collared barbet recordings.

The DFAs classified 98.2% of greater honeyguide clips as bee-eaters, and 92.9% of lesser honeyguide clips as barbets. In both cases, this was a significantly higher percentage than would be expected if recordings were randomly classified (greater honeyguide classification: Binomial Exact Test, *p*-value < 0.001; lesser honeyguide classification: Binomial Exact Test, *p*-value = 0.002).

The MLRs classified 98.8% of greater honeyguides clips as bee-eaters, and 78.6% of lesser honeyguides clips as barbets. For greater honeyguides this was significantly different from what would be expected if recordings were randomly classified (Binomial Exact Test, *p*-value < 0.001). However, for lesser honeyguides, the difference was marginally non-significantly (Binomial Exact Test, *p*-value = 0.057).

Taken together, the results from each approach indicate that honeyguides are more similar to their hosts than to each other, particularly in frequency measurements. Additionally, classification models assign the begging calls of each honeyguide to their primary host, rather than the other species of honeyguide. However, there is overlap in features between species, and the differences were only significant in the PCA and classification models, and not in DTW distances.

2.4.2 Mimicry of one or many nestlings?

2.4.2.1 Call rate analyses

In both parasite-host systems, I tested for differences in trill rate using gamma GLMMs, and I tested for differences in syllable rate using Poisson GLMMs (see Section 2.3.6.1). For greater honeyguides and bee-eaters, Z-tests on the model coefficients associated with each planned contrast (bee-eater brood vs bee-eater single, and greater honeyguide vs bee-eater brood) showed no evidence for a difference between bee-eater broods and single nestlings, or greater honeyguides and bee-eater broods, in either trill rate or syllable rate (Table 2.3, Figure 2.9). As can be seen in Figure 2.11, call rate also does not increase with brood size since bee-eater nestlings do not typically call simultaneously. However, the coefficient for syllable rate was only marginally insignificant for the contrast between greater honeyguides and little bee-eater broods, leaving open the possibility that greater honeyguides syllable rate might be slightly higher than bee-eater brood syllable rate in a larger sample.

Planned contrasts were not needed for lesser honeyguides and barbets since there were only two levels for the categories (lesser honeyguide and single barbet nestling) because nestlings in barbet broods call simultaneously (see Section 2.3.6.1). There was no evidence that lesser honeyguides differed in their trill rates or syllable rates from single barbets (Table 2.4, Figure 2.10).

Table 2.3: Results from Z-tests of GLMM coefficients for the planned contrasts (i) little bee-eater brood vs little bee-eater single nestling, and (ii) greater honeyguide vs little bee-eater brood. Contrasts were tested with both trill rate and syllable rate as response variables. The gamma distribution was used for trill rates and Poisson distribution for syllable rates.

Planned contrast	**Trill/syllable rate**	**Coefficient Estimate**	**Standard error**	***Z***	***p***
Little bee-eater brood vs little bee-eater single	Trill	0.056	0.103	0.54	0.587
	Syllable	0.003	0.043	0.07	0.944
Greater honeyguide vs little bee-eater brood	Trill	0.006	0.073	0.08	0.933
	Syllable	0.052	0.028	1.86	0.064

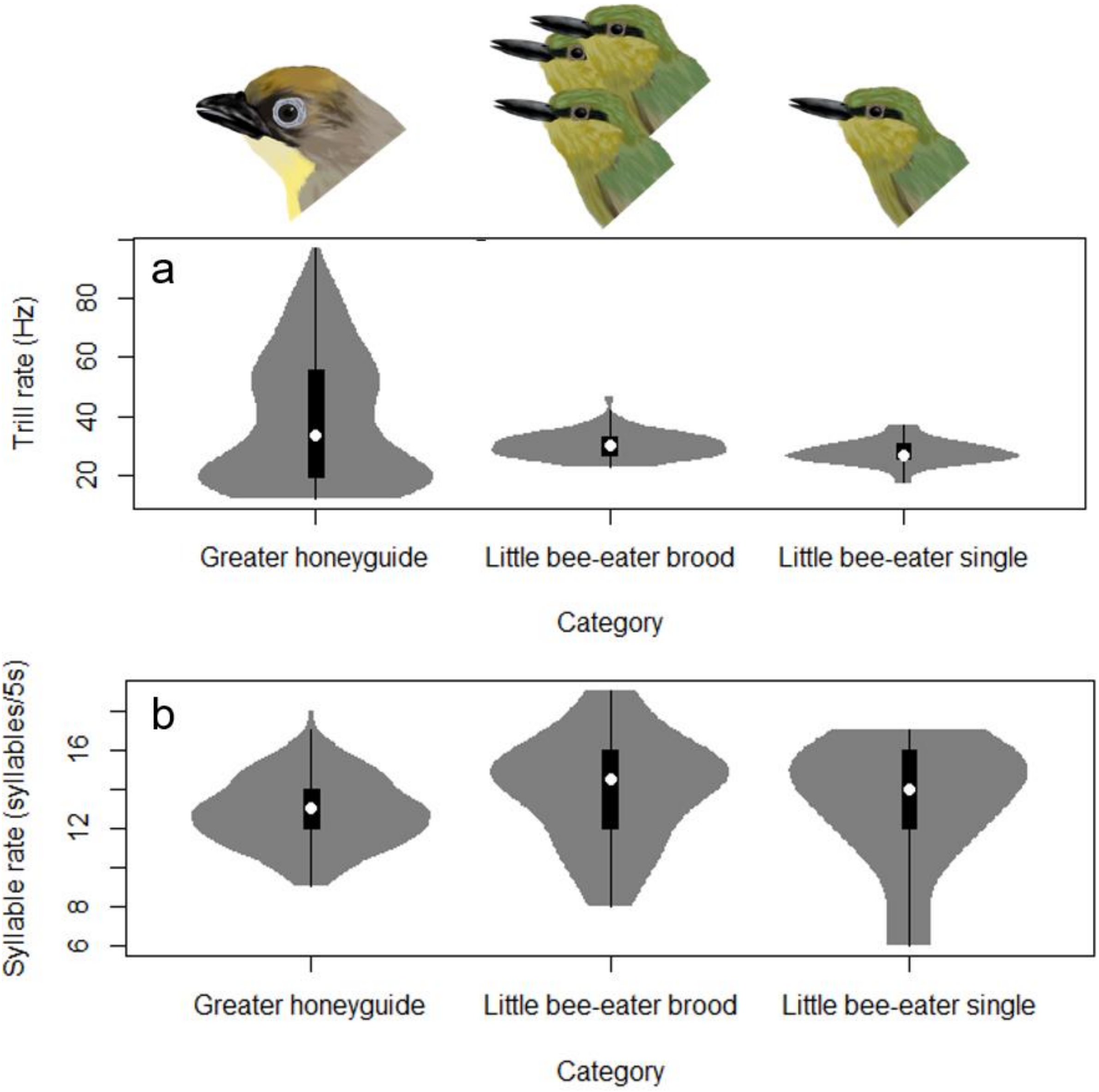


Figure 2.9: Greater honeyguides, little bee-eater broods, or single little bee-eater nestlings do not differ in the trill rate or syllable rate of their begging calls. Violin plots showing the distribution of (a) trill rate and (b) syllable rate for each category.

Table 2.4: Results from Z-tests of GLMM coefficients representing the difference in trill rate and syllable rate between lesser honeyguide and single black-collared barbet nestlings. The gamma distribution was used for trill rates and Poisson distribution was used for syllable rates.

Trill/syllable rate	Coefficient Estimate	Standard error	Z-value	*p*-value
Trill	0.010	0.122	0.08	0.933
Syllable	0.198	0.153	1.30	0.195

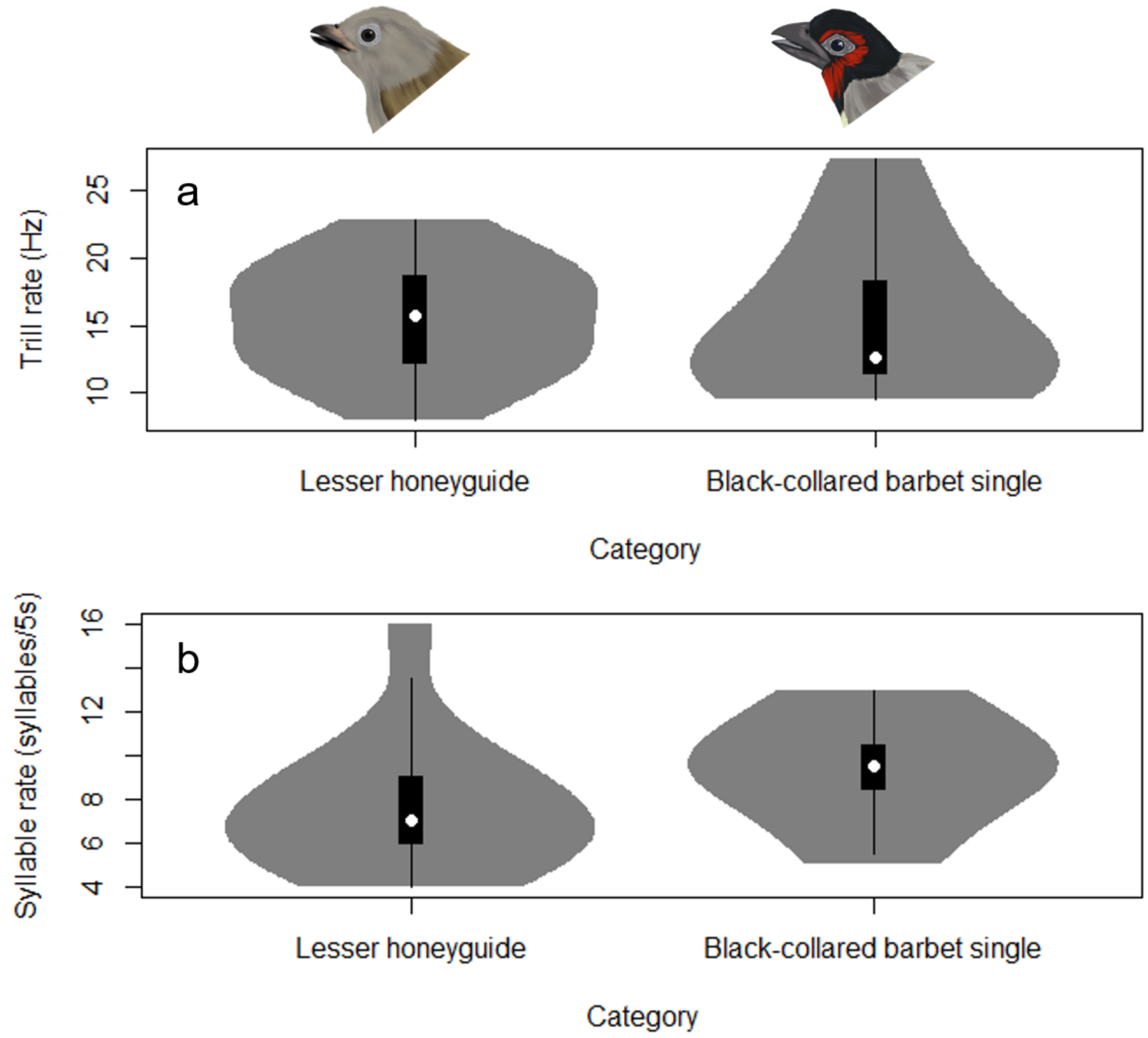


Figure 2.10: Lesser honeyguides and single black-collared barbet nestlings did not differ in the trill rate or syllable rate of their begging calls. Violin plots show the distribution of (a) trill rate and (b) syllable rate for each category.

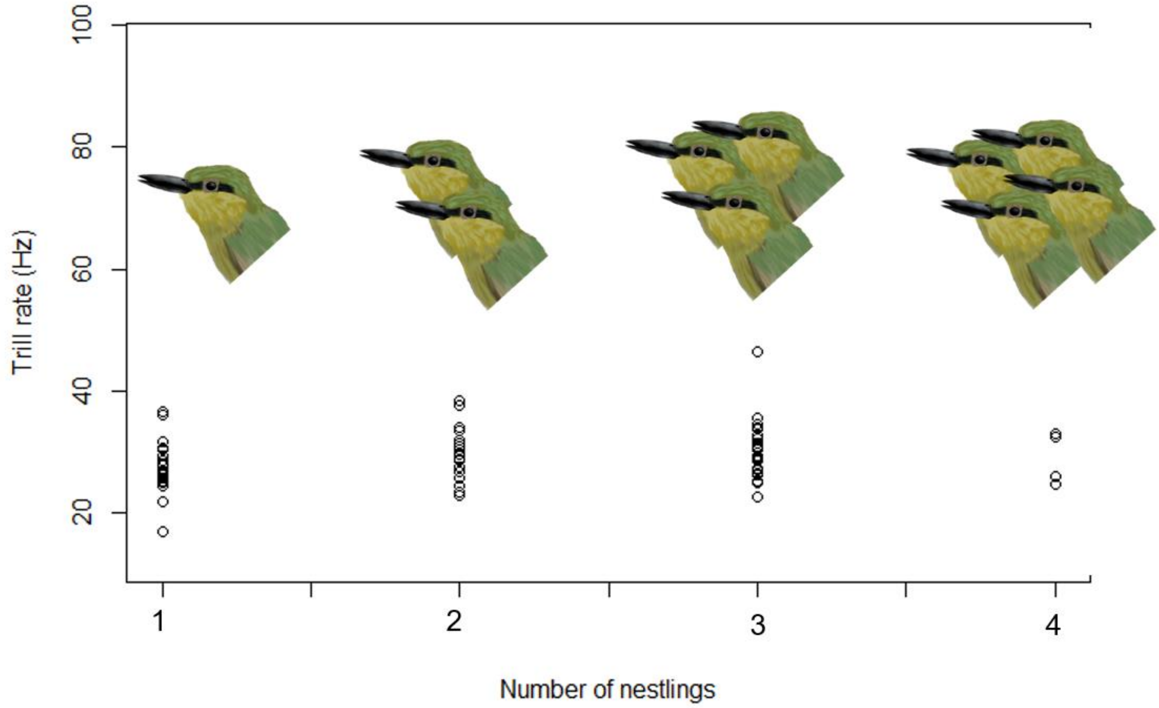


Figure 2.11: Trill rate did not differ in recordings from little bee-eater broods of different sizes, since one nestling typically begs at a time. Scatter plot of trill rate against the number of little bee-eater nestlings present in a nest.

2.4.2.2 Structural measurement analyses

First, I determined which structural features differed between host broods and single host nestlings. To do so I trained DFAs and MLRs using leave-one-out cross validation (see Section 2.3.6.1).

For bee-eater broods and single nestlings, The DFA classified begging calls to species with 77.4% accuracy, which was significantly greater than random assignment (Binomial Exact Test, p-value < 0.001). Bee-eaters also had substantially higher absolute values for the spectral entropy and time entropy coefficients in the first discriminant function (Table 2.5).

The MLR had an accuracy of 75.3%, which is also significantly greater than random assignment (Binomial Exact Test, p-value < 0.001). Median time was the only variable with a significant difference in the Type III analysis of deviance for the MLR, with mean peak frequency being the next most significant (Table 2.6). Taken together, results for bee-eaters suggest that calls from bee-eater broods and single nestlings can be accurately separated, and that the most important variables to discriminate between bee-eater broods and single nestlings are spectral entropy, time entropy, median time and mean peak frequency.

Table 2.5: Coefficients for the first discriminant function from the discriminant function analysis trained on little bee-eater broods and single nestlings. The coefficients provide a metric to assess the importance of each variable's contribution to the model.

Variable	**LD1 Coefficient**
Median frequency	-0.548
Median time	0.788
Skewness	-0.322
Spectral entropy	**10.417**
Time entropy	**1405.472**
Mean dominant frequency	-0.565
Dominant frequency range	-0.140
Modulation index	-0.025
Mean peak frequency	0.535

Table 2.6: Type III analysis of deviance table from the multinomial logistic regression model trained on little bee-eater broods and single nestlings. The significance (*p*-value) can be used to assess the importance of each variable's contribution to the model.

Variable	χ^2	**Degrees of freedom**	***p-value***
Median frequency	0.490	1	0.484
Median time	**5.937**	**1**	**0.015**
Skewness	0.874	1	0.350
Spectral entropy	-0.179	1	1.000
Time entropy	0.048	1	0.827
Mean dominant frequency	1.646	1	0.200
Dominant frequency range	0.745	1	0.388
Modulation index	1.433	1	0.231
Mean peak frequency	**2.2274**	**1**	**0.136**

The DFA trained on recordings of barbet broods and single nestlings classified clips with 93.7% accuracy, which is significantly better than if they were randomly assigned an identity (Binomial Exact Test, *p*-value < 0.001). Spectral and time entropy were identified as the most important variables for discriminating between black-collared barbet broods and single nestlings in the DFA, since they had much higher absolute values for their coefficients in the first discriminant function (Table 2.7).

The MLR classified calls with an accuracy of 92.6%, which is also significantly greater than would be expected by chance (Binomial Exact Test, *p*-value < 0.001). Spectral entropy, dominant frequency range and skewness were the most important discriminating variables in the MLR, based on the results of Type III analysis of deviance (Table 2.8). However, the differences between black-collared barbet broods and single chicks in each variable were not significant (*p*-value > 0.05; Table 2.8). In summary, both classification models classified with an accuracy greater than expected by chance and the variables spectral entropy, time entropy, dominant frequency range and skewness were the most important variables for classifying barbet broods and single nestlings.

Table 2.7: Coefficients for the first discriminant function from the discriminant function analysis trained on black-collared barbet broods and single nestlings. The coefficients provide a metric to assess the importance of each variable's contribution to the model.

Variable	**LD1 Coefficient**
Median frequency	0.331
Median time	0.082
Skewness	0.335
Spectral entropy	**-31.405**
Time entropy	**865.231**
Mean dominant frequency	0.632
Dominant frequency range	0.096
Modulation index	-0.004
Mean peak frequency	-0.328

Table 2.8: Type III analysis of deviance table from the multinomial logistic regression model trained on black-collared barbet broods and single nestlings. The significance (*p*-value) can be used to assess the importance of each variable's contribution to the model.

Variable	χ^2	**Degrees of freedom**	***p*-value**
Median frequency	-0.431	1	1.000
Median time	0.017	1	0.897
Skewness	**2.079**	**1**	**0.149**
Spectral entropy	**2.527**	**1**	**0.112**
Time entropy	0.123	1	0.726
Mean dominant frequency	1.615	1	0.204
Dominant frequency range	**2.300**	**1**	**0.130**
Modulation index	-0.057	1	1.000
Mean peak frequency	1.543	1	0.214

Next, I used LMMs to assess whether honeyguides differ from single host nestlings in the same features as host broods differ from single host nestlings, since these features are likely cues of the number of nestlings, and so may affect host parent provisioning and be exploited by honeyguides. LMMs were run with each of the most important variables for classifying barbet broods and single nestlings from the classification models (DFA and MLR) as response variables.

For barbets these were time entropy, spectral entropy, skewness, and dominant frequency range, and for bee-eaters these were time entropy, spectral entropy, median time and mean peak frequency. For each response variable, I ran models with and without the category (host brood, host single nestling, honeyguide) as a fixed effect, and recording identity nested within nest identity as a random factor except where the model fit was singular or did not converge when iterations were run instead (see Section 2.3.6.1 for details).

For the greater honeyguide and little bee-eater recordings, all the models had either a singular fit or failed to converge when recording identity was included in the random effects structure, except in the models with time entropy as the response. With respect to time entropy, there was no evidence for a difference between greater honeyguides, little bee-eater broods, and little bee-eater single nestlings, since the model without category had a significantly better fit than the model with category included (ΔAICc = 32.48). For the remaining response variables (spectral entropy, median time, mean peak frequency), the number of iterations where the models with category included as a fixed factor had a significantly better fit (ΔAICc > 2) than the models that excluded category was not more than the 95% confidence threshold for each of the other response variables (Table 8). Together these results indicate that overall, greater honeyguides begging calls do not seem to differ from the begging calls of either single host nestlings or host broods.

Table 2.3: The number of iterations, out of 100, where the model that included category (greater honeyguide, little bee-eater brood or little bee-eater single nestling) as a fixed effect (test model) was significantly better fitting (ΔAICc > 2) than the model that did not include category (null model).

Variable	**Number of iterations where test model fit significantly better than null model (ΔAICc > 2)**
Spectral entropy	0
Median time	19
Mean peak frequency	34

In the lesser honeyguide and barbet recordings, the only response variable in which the models did not fail to converge, or had a singular fit, was skewness. With skewness as the response, the model with category as a fixed effect had a significantly better fit than the model without category (ΔAICc = 4.32). Pairwise comparisons using Tukey’s significance tests indicated that there was only a significant difference between the clips of single barbet nestlings and barbet broods (estimated difference in marginal means = 1.470, t_{69} = 2.742, *p*-value = 0.021; Figure 2.12). Lesser honeyguide clips were intermediate between them and overlap with both black-collared barbet single nestlings and broods in their 95% confidence interval for the estimated marginal means (Figure 2.12). Models for each of the other response variables were either not able to converge or had a singular fit, when recording identity was included in the random effects structure. When time entropy was a response variable, in none of the 100 iterations did the model with category as a fixed factor have a better fit than the model with category excluded (Table 2.10). Similarly, when spectral entropy was a response variable, in only 7 of the 100 iterations did the model with category included have a significantly better fit (Table 2.10). Therefore, there is no evidence that there are any differences between the categories (barbet brood, barbet single nestling, and lesser honeyguide) in both time and spectral entropy. With dominant frequency range as the response variable, the model with category included fit better in 69 of the 100 iterations. This provides some evidence for a difference in dominant frequency range, but the difference was still not significant at a 95% confidence threshold. Together these results indicate that only skewness differs significantly between categories, and that overall, lesser honeyguides begging calls do not seem to differ from the begging calls of either single hosts or host broods.

Table 2.10: The number of iterations, out of 100, where the model which included category (lesser honeyguide, black-collared barbet brood or black-collared barbet single nestling) as a fixed effect (test model) was significantly better fitting (ΔAICc > 2) than the model that did not include category (null model).

Variable	# iterations where test model fit better than null model (ΔAICc > 2, 100 iterations)
Time entropy	0
Spectral entropy	7
Dominant frequency range	69

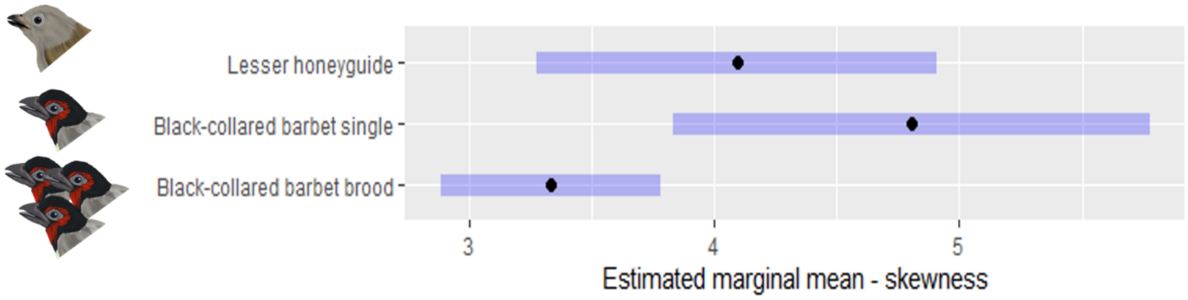


Figure 2.12: Estimated marginal means calculated from a linear mixed-effect model with skewness as the response, category (black-collared barbet brood, black-collared barbet single nestling, and lesser honeyguide) as a fixed effect and the recording ID nested within nest ID as random effects. Error bars indicate 95% confidence intervals for each marginal mean.

Together these results show that 1) neither honeyguide species differed in call or syllable rate from single host nestling nor from host broods, and 2) that the structural features of begging calls of neither honeyguide species were more similar to those of a host brood than those of a single host nestling. This suggests that greater and lesser honeyguides do not mimic the begging calls of specifically a brood of host nestlings.

2.5 Discussion

In this chapter I tested 1) whether two species of brood-parasitic honeyguides, the greater and lesser honeyguides, mimic the begging calls of their primary host, and 2) whether they mimic specifically a brood of host chicks rather than a single host chick. My analyses showed that the begging calls of each honeyguide species are 1) more similar in structure to those of their hosts than to those of the other honeyguide species, and 2) no more similar in rate or structure to host broods than they are to single host nestlings. This provides the first quantitative evidence of host begging call mimicry by these parasitic species. However, I found no evidence that these specifically mimic broods of their hosts, either through call rate matching or matching of any other structural features. This implies that other features of honeyguide begging calls might be responsible for the high rate of provisioning they elicit from their host parents.

2.5.1 Mimicry of primary host species

The results indicated that the begging calls of each honeyguide species are generally more similar to those of their primary host species than to those of the other honeyguide species, with some overlap in features between all the species studied (Figures 2.5–2.8). Each species has a broadly similar begging call structure during later (stage 3) nestling development, with a trill syllable and sometimes a shorter syllable in between trill syllables (Blair et al. MS). Each honeyguide appeared match the pitch of its hosts as well as the call rate of both trills and syllables. Greater honeyguides and little bee-eaters have generally higher-pitched begging calls with a faster trill and syllable rate than lesser honeyguides and black-collared barbets. These results are consistent with the hypothesis that each honeyguide mimics its primary host's begging calls, and that the structure of honeyguide begging calls is not only the result of the ancestral begging call state in honeyguides. However, it is necessary to exclude any other potential causes of similarity in each host-parasite pair; I will consider each alternative hypothesis in turn.

First, similarity in begging calls between host-parasite pairs could arise through convergence rather than mimicry. If the physical environment of the nest favours certain acoustic properties of begging calls, parasites and their hosts may converge because they have identical nest environments. I found that the two host species, the distantly related black-collared barbet and little bee-eater, have a broadly similar begging call structure to each other, with rolling trill syllables. However, despite showing superficial similarities in structure, each host species is significantly different from each other in numerous acoustic traits (Figures 2.5 and 2.6). The superficial similarity between the distantly related hosts may suggest that trilling calls in general are adaptive in hole-nesting birds. In theory, nestlings of hole-nesting birds are able to make louder and more conspicuous begging calls than cup-nesting birds, since the sound is reflected by the walls of the nest chamber and attenuates quickly outside of the nest chamber (Haskell, 2002). Having a “rolling” call structure with trill elements may be more conspicuous than simple single syllable calls and may also elicit more provisioning if there is a widespread sensory bias in parents for faster begging call rates (Butchart et al., 2003; Davies, Kilner & Noble, 1998; Kilner, Noble & Davies, 1999; Madden & Davies, 2006). If selection imposed by begging calls attracting the attention of predators is relaxed in hole-nests, then this may allow hole-nesting birds to have these favourable call types. This requires further study, ideally by comparing the begging calls of hole-nesting birds and their open-nesting relatives. However, the close matching between each honeyguide and its host cannot be explained entirely by shared ecology. While we lack direct data on this, it is difficult to believe that the similarity between each host – parasite pair, and the differences between the honeyguides differences are the result of similar pressure from predation experienced by each host – parasite pair. Moreover, even though one host species nests in tree cavities and the other in terrestrial burrows, both systems involve calling in small, enclosed spaces, suggesting that the acoustic environment in each species’ nest is unlikely to be sufficiently different to account for the acoustic similarity between each host-parasite pair. This view concurs with that of Jamie & Kilner (2017) who also suggested that acoustic environment in the nest and predation risk cannot explain the close matching between hosts and brood parasites in systems where begging call mimicry is suspected.

Second, we should consider whether the observed similarity between each honeyguide and its primary host species is the result of chance. In other words, even in the absence of selection imposed by host parents, it is possible that drift, unrelated selection pressures, or some constraint may happen to make honeyguide begging calls similar to those of their hosts. For example, there is evidence that the calls greater honeyguides use to lead humans to bees’ nests’ (guiding calls) as part of a cooperative relationship with people, develop from their begging calls (Blair et al. MS). If so then selection on the structure of guiding calls may affect the structure of greater honeyguide begging calls, leading them to diverge from closely related honeyguide species (such as lesser honeyguides) and by chance more similar to little bee-eaters. However, this seems improbable given that guiding calls develop from begging calls and not vice-versa. Moreover, the results of McClean’s (2020) playback experiments demonstrate that the provisioning rates of the honeyguides’ host parents are lower when the begging calls of a control species (i.e. not a host nestling or honeyguide nestling) are played. This suggests that the host parents respond specifically to calls that sound like their own chicks, and thus likely impose selection on honeyguide begging calls, since insufficient provisioning would affect their survival rate. Therefore, it is unlikely that the similarity between each host-parasite pair is due to chance and not selection imposed by host parents.

Thus, the most likely explanation for the observed begging call similarity between each honeyguide and their hosts is that there has been selection on honeyguides by host parents to sound like their own nestlings. Mimicry would allow honeyguides to avoid detection by host parents and/or ensure that they receive adequate provisioning. To be certain that mimicry is occurring, we would need to demonstrate that the host parents can either detect and reject and/or provision less food to poorly-mimetic parasitic chicks, in at least some cases. Although this has not been tested yet, McClean (2020) did find lower feeding rates when playback of miombo blue-eared starling (*Lamprotornis chloropterus elisabeth*) was used at barbet nests. Lower provisioning rates to poorly-mimetic parasitic chicks could also arise because host parents have a sensory bias towards particular begging call features, and thus impose parallel selection on both their own nestlings and honeyguide nestlings to exhibit similar begging calls. If there is a sensory bias in the host parent, selection is still imposed by the receiver (as in mimicry), but the receiver is not necessarily responding because of the perceived similarity, but because of its own inherent biases (De Jager & Anderson, 2019; Grim, 2004). Whether this still constitutes mimicry is a topic of debate (De Jager & Anderson, 2019; Grim, 2004).

In this study, the strongest evidence for mimicry was found for begging call frequency, since (of the variables assessed) variables associated with frequency were the most useful to separate the host-parasite pairs (Table S2.1). This accords with prior work finding similar frequencies in the begging calls of hosts and parasites in many systems where mimicry is exhibited or suspected (Jamie et al., 2020; Langmore et al., 2008; Ursino et al., 2018). This make sense since many birds are thought to have refined discrimination ability between sound frequencies to process complex songs (Bregman, Patel & Gentner, 2016; Hoeschele, 2017), making frequency likely a highly detectible feature that hosts can use to identify strange begging calls that may indicate parasitism.

Yet despite their similarity particularly in frequency, honeyguide begging calls were not perfect matches to the begging calls of their primary host. Some calls in both honeyguides fell outside the range of variation of their respective hosts (Figures 2.6–2.7), suggesting that mimicry of host nestlings is imperfect. One potential explanation for such imperfection may be Weber's Law of proportional processing. Weber's Law states that receiver perception processes stimuli proportionally, rather than absolutely (Fechner 1966; Weber 1934). Therefore, to evade detection by receivers, mimics of complex traits may not need to be as good of a match for their model as mimics of simpler traits (Dixit et al. 2021). The begging calls of all species in this study are relatively complex, compared to those of other bird species, as they have two different syllable types and are variable in structure. Often, bird nestlings have simple begging calls with only one syllable type. Therefore, since the begging calls of the host nestlings are comparatively complex, honeyguides may not need to be perfect mimics to evade detection by their host parents. The prediction that honeyguides evade detection despite imperfect begging calls could be tested in future fieldwork by comparing the responses of host parents to honeyguide begging calls that are perfect and imperfect matches. The absolute degree of imperfection of simple stage 1 begging calls could also be compared to complex stage 3 begging calls to test the prediction that simple calls need to be better mimicked to evade detection, following Weber's Law. However, the differences in selection pressures at each age need to be considered since there is more to gain by the host parents if chicks are rejected at a younger age.

Imperfect mimicry in begging calls may also arise because both species of honeyguide examined in this study parasitise multiple host species. Therefore, multiple species may exert selection on honeyguide begging calls, leading to a call which generally mimics a range of species and is an imperfect mimic of each. However, at any one location, honeyguides often appear to have a primary host that is most frequently parasitised, and further work will need to assess whether there is evidence for mimicry of secondary hosts as well. This hypothesis is perhaps more likely to apply to lesser honeyguides, since this species exclusively parasitises African barbets (family Lybiidae) (Short & Horne, 2001) and so a generalist begging call may elicit sufficient provisioning for nestling survival in multiple closely-related hosts if these share similar features. I could only find one recording of the begging call in another *Lybius* species. This is of Vieillot's barbet (*Lybius vieilloti*), recorded by Bram Piot in Senegal (www.xeno-canto.org/385674), which sounds remarkably similar to black-collared barbet begging calls. Generalist begging calls may even act as an important restriction that prevents lesser honeyguides from parasitising a wider range of species. By contrast, greater honeyguides parasitise a wide range of distantly-related host species which include bee-eaters, kingfishers, hoopoes, woodhoopoes, swallows and starlings. Previous writers have also commented on the apparently close mimicry by greater honeyguide nestlings of red-throated bee-eaters and green woodhoopoes (Fry 1974; Jubb, 1966). However, since these are all cavity-nesting birds, there may still be general structural similarities that allow the honeyguides to ensure sufficient provisioning in secondary host nests. Additionally, it is possible that honeyguides could plastically adjust their begging calls to those of secondary hosts. Since honeyguides are raised alone, they are not exposed to the begging calls of their host's nestlings, and thus cannot directly mimic their calls by listening and trying to match their sound. However, in other generalist brood parasites that evict host young and so are raised alone, social shaping by the host parents (i.e. parasites altering their begging calls in response to which variants elicit the most food) generates mimicry of more than one species. For example, two cuckoo species, common cuckoo and Horsfield's bronze-cuckoo, plastically alter their begging calls through experience to better match those of their hosts (Madden & Davies, 2006; Langmore et al., 2008). Common cuckoos alter their call rate to match that of a host brood (Madden & Davies, 2006), whereas Horsefield's bronze-cuckoos alter their call duration and frequency to match those of their hosts (Langmore et al., 2008). Honeyguides may plausibly use a similar mechanism of plastically altering their calls in response to shaping by their host parents to mimic a wider array of species, allowing them to retain a generalist innate begging call that approximates that of multiple hosts before being plastically refined to particular species.

This study specifically analysed the begging calls of older nestlings, and we still need to test for mimicry in the calls of younger nestlings, particularly since the structure of the begging calls changes greatly during development. Hatchlings of both honeyguide species give simple single-syllable calls, which progress to complex multisyllabic rolling calls via an intermediate stage (See Figure 2.1). Noh et al. (2021) suggested that there may be stronger selection for mimicry in younger nestlings since rejection by the host parents based on begging calls is more likely to occur at this stage. Moreover, since the calls of younger nestlings are simpler, Weber's Law would also predict stronger selection for mimicry, resulting in high fidelity mimicry, since differences between honeyguide and host begging calls would be easier to detect by the host parent (Dixit et al., 2021). Despite not having quantitatively analysed the recordings of younger nestlings, based on the small sample of recordings I have listened to, honeyguides do appear to be good mimics at this stage as well, but the human ear is still able to reliably separate honeyguide and host begging calls based on slight differences in their timbre, which is influenced by irregular vibrations of the vocal folds or supraglottal oscillators, leading to non-linear vocal phenomena (Anikin, 2020), and is not related to the pitch and temporal arrangement of the vocalisations.

2.5.2 Call rate matching and brood mimicry

It has been previously suspected that honeyguides mimic the begging calls of host broods (Fry 1974; Jubb, 1966; McClean, 2020), much as has been demonstrated for other brood-parasitic species such as common cuckoo and various cowbird species (Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2011). Prior experimental findings in honeyguides supported this idea, since single honeyguide chicks (of both species considered here) were fed at approximately the same rate as a host brood, and at a higher rate than a single host chick, and playback experiments isolating the effect of begging calls alone were able to replicate this pattern (McClean, 2020). However, my results in this chapter suggest that there is no acoustic evidence that brood mimicry drives this effect. All spectral and temporal structural features of honeyguide begging calls did not differ from those of single host nestlings in those features that were most useful in discriminating between single host nestlings and host broods. This is inconsistent with the hypothesis that honeyguides specifically mimic host broods.

In other systems, the only acoustic mechanism that has been demonstrated to increase provisioning by host parents to brood-parasitic nestlings is elevated call rate, likely to mimic the sound of multiple individuals in a brood. However, call rate only provides an accurate cue of the number of nestlings requiring food if nestlings call simultaneously. In most recordings of little bee-eater broods, only a single nestling was calling at a time. Accordingly, I found no additive effect of multiple chicks calling on call rate in little bee-eaters (Figure 2.11). I also found no detectable difference between recordings of broods and single nestlings of little bee-eaters for any of the structural variables measured (Tables 2.5 & 2.6). Even though bee-eaters may not beg simultaneously, begging calls of bee-eaters in a brood may still vary with the number of nestmates since there is more competition when there are more nestlings in a brood. However, the results indicate that there is no difference even in the calls of single nestlings in a brood or alone. Black-collared barbet nestlings, on the other hand, call simultaneously, often leading to a wall of cacophonous noise. Correspondingly, in this system the difference between a black-collared barbet brood and a single nestling was more detectable in the structural variables measured (Tables 2.7 & 2.8). However, I found no evidence that lesser honeyguides mimic any of the distinctive acoustic features of black-collared barbet broods: there was no detectable difference between lesser honeyguides and single barbet nestlings in those variables that were useful to discriminate between barbet broods and single nestlings (Table 2.10 & Figure 2.12). In summary, there is no evidence that honeyguides mimic specifically either the call rate or any other feature correlated with the presence of multiple host nestlings. This suggests that some other novel mechanism must be responsible for elevated provisioning in this system.

Why do honeyguides not simply increase their calling rates like cuckoos and cowbirds do? Thus far, high call rates by brood parasites to increase provisioning have been observed specifically in parasites that target species with simple begging call structures (Butchart et al., 2003; Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2013; Kilner, Noble & Davies, 1999; Madden & Davies, 2006). As mentioned earlier, the hosts of both honeyguides have complex begging calls, which includes a trilled syllable type. Trill rate can be constrained by the vocal tract, and the maximum trill rate is related to the frequency bandwidth (Podos, 1997). The trill rate exhibited by the hosts may be at the upper boundary of the trill rates that honeyguides are able to produce. If so then honeyguides may be mechanistically unable to use increased trill rates to elicit higher rates provisioning. In the songs of species within the songbird superfamily Emberizoidea (thus distantly related to honeyguides), Podos (1997) illustrated that frequency bandwidth appeared to constrain trill rate, with wider bandwidths corresponding with lower maximum trill rates (Figure 2.13). To my knowledge this has not yet been examined in other bird taxa, but it seems likely that similar constraints are present. The threshold values may perhaps even be similar across other birds, since Podos (1997) found that the bird size did not affect this pattern. If the mean trill rates and dominant frequency range (a measure of frequency bandwidth) for each honeyguide and host species are plotted on the same axes as the threshold determined by Podos (1997), the values for each species are above the threshold (Figure 2.13), indicating that it is plausible that the trill rates are at the upper limits of the possible trill rate. However, studies examining maximum trill rates across a wider range of birds, especially non-passerines, are necessary to assess the physical limits of trill rates. Non-mutually exclusively, it is also possible that host hearing lacks the temporal resolution to be able to resolve higher trill rates than those observed. Therefore, there may not be selection for begging calls at higher trill rates since this is not detectible by hosts and so has no effect on host provisioning, even if physically possible. The auditory temporal resolution of birds is variable and not well understood in most birds. In songbirds, there is evidence for a trade-off between frequency and temporal resolution (Henry et al., 2011). If this is the case more broadly in birds, or at least in the host species in this study, selection for precise frequency resolution to detect unusual begging calls associated with parasites may be constraining the host parent temporal resolution.

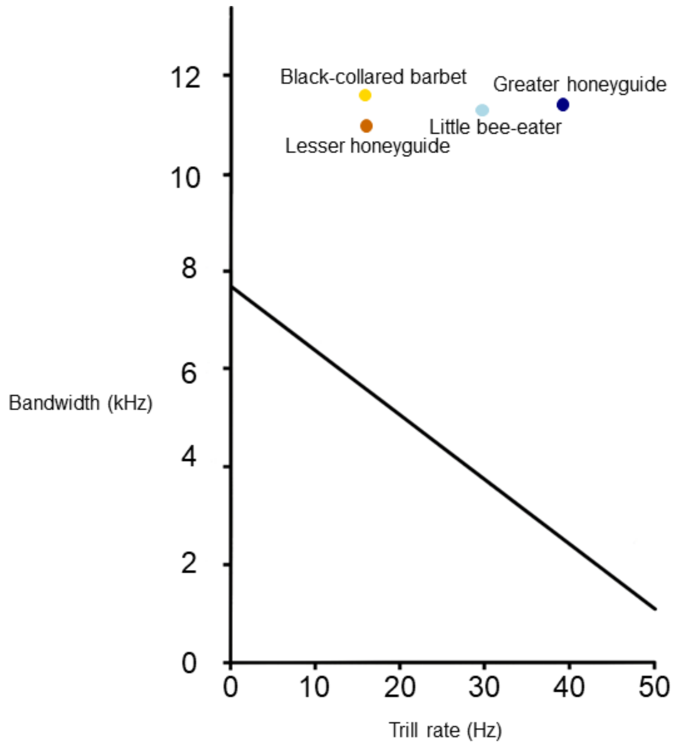


Figure 2.13: Are the trill rates of honeyguides and their hosts at their physical limits? Mean trill rates and mean dominant frequency range (a measure of bandwidth) for each species, represented by each dot with the species indicated by a label alongside. The diagonal line represents the threshold determined by Podos (1997) for the maximum trill rate in bunting and sparrows of the superfamily Emberizoidea, the only group for which maximum trill rates has been assessed, which has an inverse relationship with frequency bandwidth.

The ancestral state of a brood parasite’s begging call may also play a role in which mechanism is used to increase provisioning. Perhaps the ancestral state of honeyguide begging calls already exhibited a feature other than high call rate which affected provisioning by host parents, and this feature was exaggerated instead of call rate. For example, in brown-headed cowbirds (*Moluthrus ater*), the ancestral begging call state is inferred to have had and exaggerated call rate compared to its hosts (Rivers et al., 2013), since the cowbirds’ closest non-parasitic relatives call at similarly high call rates (Rivers et al., 2013). Begging calls of red-winged blackbirds (*Agelaius phoeniceus*), close relatives of brown-headed cowbirds, even elicited similar levels of provisioning to the calls of brown-headed cowbirds (Rivers et al., 2013). Therefore, the brown-headed cowbird was likely preadapted for host exploitation by having a high call rate, relative to the nestlings of their hosts, which helped to increase host provisioning. Honeyguide begging calls may have been similarly preadapted to exploit a sensory bias present in its host, but in a feature other than call rate. In summary, bird parents may use multiple acoustic cues to infer the number of nestlings needing food, and parasitic ancestry may shape which cue is exploited by their brood parasites.

In this chapter I only assessed the spectral and temporal structure of the begging calls. However, a possible feature that honeyguides could alter without changing the structure is the perceived harshness of their begging calls. Harshness is affected by non-linear dynamics in the vocal tract, and non-linear vocal phenomena (NLP) signal states of high arousal in many contexts and in widely diverse animal taxa (Anikin, 2021). Although the responses of parents to NLP in begging calls has not been tested, it is a plausible mechanism that brood-parasitic nestlings could use to increase provisioning. In chapter 3 I test this hypothesis.

2.5.3 Conclusion

I provide evidence that greater and lesser honeyguides likely mimic their primary hosts, little bee-eaters and black-collared barbets respectively. This suggests that in these systems, mimicry is likely essential to avoid detection and/or obtain adequate provisioning. The acoustic mechanism driving elevated provisioning levels to honeyguide nestlings remains elusive, but (contrary to previous suggestions) it does not appear to be brood mimicry, since neither call rate nor any structural features of begging calls that distinguished host broods from single host nestlings were elevated in honeyguides. My analysis of honeyguide and host begging calls suggest that a supernormal call rate (the only acoustic mechanism that has been shown in other systems to increase provisioning to brood parasites) does not appear to be present in honeyguides, perhaps because call rates are already at their upper physical limit. Similarly, I found no evidence of supernormal stimulus in any other structural features. Therefore, honeyguides must use another mechanism to increase provisioning that has not yet been demonstrated in other brood-parasitic systems. The use of NLP by honeyguides offers an attractive hypothesis when considering the structure of host and honeyguide begging calls, since it is a feature that is used to heighten the intensity of a signal across many different contexts and should be investigated further. In summary, this study provides quantitative support for mimicry in a system where mimicry was suspected but not directly assessed. Additionally, it suggests that there are multiple acoustic mechanisms which brood parasites can use to manipulate the provisioning behaviour of their hosts.

CHAPTER 3

Could non-linear vocal phenomena facilitate host manipulation by brood parasites?

3.1 Abstract

The nestlings of avian brood parasites often have food requirements that exceed those of the host nestlings, requiring them to alter their begging calls to manipulate their host parents into feeding them more. Non-linear vocal phenomena (NLP), which are caused by perturbations of the typical vocal fold vibrations, signal parental care requirements in the vocalisations of some mammal species. However, whether they have any signalling function in the begging calls of nestling birds has not been explored. If they signal need in nestling birds, they may offer a mechanism for brood parasites to manipulate host provisioning. Greater (*Indicator indicator*) and lesser (*I. minor*) honeyguides are both brood parasites that use their begging calls to manipulate provisioning by their host parents. In this chapter, I examine whether there is evidence that honeyguides use NLP as a mechanism for host manipulation. I measured variables associated with the presence of NLP in the begging calls of both honeyguides and of broods and single nestlings of their respective primary hosts, the little bee-eater (*Merops pusillus*) and black-collared barbet (*Lybius torquatus*). In each parasite-host pair, I found no significant differences between single host nestlings and honeyguide nestlings in any of the variables associated with NLP. Begging calls of little bee-eater broods had significantly higher amplitude modulation frequency than greater honeyguide begging calls, but not single bee-eater nestlings. Black-collared barbet broods had significantly higher perceived roughness than single barbet nestlings, but not lesser honeyguides. Additionally, I conducted a playback experiment in the field in the Choma district, Zambia, to test whether features of the amplitude envelope, such as amplitude modulation (one type of NLP) and the resulting perceived roughness, affect provisioning by host parents. To do so I manipulated recordings of single lesser honeyguides and black-collared barbet nestlings by swapping their amplitude envelopes. I then played these back, along with unmanipulated controls, at natural host nests, and recorded the provisioning rate of the host parents. I found no significant difference in provisioning rate between any of the playback treatments, suggesting that amplitude modulation, at least in the frequency range I manipulated, does not influence parental provisioning. Overall, my results are inconclusive as to whether NLP are used by honeyguides to manipulate provisioning by their primary hosts but suggest that it probably does not. Moreover, the lack of a difference in provisioning rates even in control treatment calls fails to replicate differences observed in a previous study, which might be due to interannual differences in environmental conditions influencing provisioning behaviour. Nonetheless, NLP should be explored further as a potential signalling feature in begging calls and other bird vocalisations.

3.2 Introduction

Avian brood parasites, birds that lay their eggs in the nests of other birds to forgo the costs of parental care, often have different food requirements to nestlings of their host species (Davies, Kilner & Noble, 1998; Kilner, Noble & Davies, 1999; McClean, 2020). To obtain more food, brood parasites often manipulate the provisioning rate of host parents by tapping into the existing communication systems between host parents and their nestlings (Davies, Kilner & Noble, 1998). Begging calls are one of the key ways that bird nestlings signal their food needs to parents (Johnstone & Godfrey, 2002), and consequently many brood parasites alter aspects of their begging calls to increase provisioning by host parents (Davies, Kilner & Noble, 1998; Dearborn & Liechtenstein, 2002; Kilner, Noble & Davies, 1999; Redondo & Zoñiga, 2002)

Techniques to increase provisioning differ depending on whether the brood-parasitic chick is the sole occupant of the nest. Non-evicting brood parasites, which are raised alongside host nestlings, can increase their food intake by outcompeting host nestlings when a parent brings food to the nest. For example, brown-headed cowbirds (*Molothrus ater*) use their begging calls to increase provisioning to the brood as a whole but are able to outcompete the host nestlings for the food provisioned to the brood (Hauber & Ramsey, 2003; Hoover & Reetz, 2006; Kilner, Madden & Hauber, 2004, Rivers, 2006; Ursino et al., 2011). It is therefore easier for non-evicting brood parasites to obtain more food than evicting parasites, since they benefit from the begging signals of a whole brood, provided that they outcompete host nestlings. By contrast, evicting brood parasites (which remove the host nestlings and are raised alone) need to use their own begging signals alone to increase provisioning by their host parents. They may do this by mimicking cues host parents associate with a brood of host nestlings (Davies, Kilner & Noble, 1998). Alternatively, they may exploit sensory biases in the host parents to create supernormal stimuli that exceed the stimuli of host broods, for example by exaggerating features associated with need (Kilner, Noble & Davies, 1999).

Begging call features that have been demonstrated to be associated with higher levels of provisioning in birds include higher call rate, narrower frequency range, higher peak frequency, longer syllable duration and higher amplitude (see Table 2.1 in Chapter 1; Sacchi et al., 2002; Hauber & Ramsey, 2003; Anderson, 2010, Corney & Barber 2018). For each of these variables, higher provisioning may result either because the acoustic feature signals that the nestlings need more food, or because it is a cue that the parents associate with the number of nestlings that need to be fed. In brood parasites, call rate is the only acoustic feature that has been demonstrated to substantially increase host provisioning. (Davies, Kilner & Noble, 1998; Kilner, Noble & Davies, 1999; Gloag & Kacelnik, 2013). This is likely because higher call rates are associated with more nestlings begging simultaneously in the nest (Davies, Kilner & Noble, 1998), and are so an example of brood mimicry. Nonetheless, it is possible that brood parasites may also exploit other acoustic features to elicit more food, but that this has been overlooked so far.

Greater and lesser honeyguides (*Indicator indicator* and *I. minor*), two closely related brood-parasitic bird species, provide a case where manipulation of provisioning by their primary hosts is not the result of increased call rate (see Chapter 2). Both these honeyguide species require more food than a single nestling of their primary host species (see Chapter 2), respectively little bee-eater (*Merops pusillus*) and black-collared barbet (*Lybius torquatus*). A playback experiment by McClean (2020) demonstrated that for both honeyguide species, provisioning rate of their primary host was significantly higher when begging calls of the honeyguide were played compared to when the begging calls of a single host nestling were played. Both honeyguides are raised alone, since newly-hatched honeyguide chicks kill their host nestmates using sharp bill hooks, which they use to grab and shake them (Spottiswoode & Koorevaar, 2012). Neither honeyguide species has higher call rates than its primary hosts (Chapter 2, this dissertation), making it unlikely that honeyguides use call rate to manipulate provisioning by their host parents. Additionally, honeyguide begging calls do not differ from the begging calls of single host nestlings in those temporal or structural features that are useful for discriminating between calls from single host nestlings or host broods. It is therefore unlikely that honeyguides mimic these features of host broods (Chapter 2, this dissertation). Instead some other mechanism, independent of begging call structure, must be responsible for manipulating the provisioning rate of their host parents.

One possible mechanism that brood parasites could use to increase provisioning rate by their hosts is to incorporate non-linear vocal phenomena (NLP). NLP are acoustic irregularities caused by perturbations of the typical vibration of the vocal folds in animals, creating harshness or roughness in the sound of the vocalisations (Anikin, 2020). Common types of NLP present in animal vocalisations are deterministic chaos, subharmonics, amplitude modulation, and pitch jumps (Table 3.1; Anikin, 2020; Anikin et al., 2021). These have been observed to signal states of high arousal in signals of both positive and negative valency (Anikin, Pisanski & Reby, 2020) by a variety of animals from frogs to humans (Chen et al., 2022; Anikin et al., 2021), and are found in vocalisations of animals used in many different contexts (Chen et al., 2022; Digby et al., 2013; Fernández-Vargas & Johnstone, 2015; Marx et al., 2021; Pisanski et al., 2021; Thévenet et al, 2023; Townsend & Manser, 2010; Serrano et al., 2019). Specifically, NLP is suspected to function in signalling intensity in vocalisations associated with alarm (Townsend & Manser, 2010), distress (Pisanski et al., 2021), stress (Marx et al., 2021), territory defence (Digby et al., 2013; Serrano et al., 2019), and sexual contexts (Chen et al., 2022; Fernández-Vargas & Johnstone, 2015; Serrano et al., 2019).

Table 3.1. Types of non-linear vocal phenomena (NLP) along with their causes in the vocal tract and the effect that they have on the vocalisation produced (adapted from Anikin, 2020).

Type of NLP	Cause	Effect
Deterministic chaos	Chaotic vibration of the vocal folds	Harsh broadband sound, that resembles noise, but

		still retains some harmonic structure
Subharmonics	Vibration of one vocal fold at exactly two or three times the frequency of the other vocal fold	Sidebands to each harmonic half or a third of the way between harmonics
Amplitude modulation	Low frequency vibration of additional supraglottal oscillators	Sidebands to each harmonic, similar to subharmonics, but usually closer to the harmonic than subharmonics
Pitch jumps	Abrupt discontinuities in pitch	Steep changes in the fundamental frequency and associated harmonics
Bifurcations	Dependent of the types of NLP that are changing	Changes in type of NLP present

The use of NLP in vocalisations associated with eliciting parental care has only been examined in the infant vocalisations of mammalian species, including humans, chimpanzees and bonobos (*Pan* spp.) (Thévenet et al, 2023) and the giant panda (*Ailuropoda melanoleuca*) (Stoeger et al., 2012). In humans, infant cries act as a signal that they need some form of parental care. The level of distress experienced by a human infant is proportional to the pitch and the NLP present in their cry (Stoeger et al., 2012; Thévenet et al, 2023). Since NLP is used to signal the level of arousal in mammalian young, it is plausible that NLP may also be present in the begging calls of bird nestlings, and act as a signal for how much food a bird parent needs to provide its nestlings.

There is some evidence that NLP may even communicate the state of arousal when the emitter and receiver are distantly related species. One example is that Nile crocodiles (*Crocodylus niloticus*) are attracted to the cries of human, chimpanzee and bonobo infants, and their response is dependent on the quantity of NLP in the cry (Thévenet et al, 2023). Another example is communication between dogs and their owners. Humans are able to assess the level of distress in dogs through the NLP present in their whines, with humans associating whines with higher levels of NLP with increased distress (Massenet et al., 2022). This illustrates that very distantly related animals can respond to NLP in a similar manner (Thévenet et al, 2023), and suggests that the response to NLP is deeply conserved in vertebrates. It also raises the question whether generalist interspecific brood parasites, such as honeyguides, may use NLP to exploit their multiple hosts, since it may be effective across a wide range of species.

Honeyguides appear to mimic the begging call structure of a single nestling of their primary host, and the spectral or temporal structure of their calls do not explain the higher rate of provisioning they receive from their host parents (Chapter 2). Since honeyguides appear to mimic the pitch and temporal structure of their host begging calls, these are likely important cues of identity used by their host parents, and the presence of NLP in honeyguide begging calls may only be effective if the host parents first accept that the call is coming from their own species. Since NLP may be added or removed without changing the pitch or temporal structure of the vocalisation, it is an ideal candidate for a mechanism by which honeyguides could manipulate provisioning. An analogous case is the response of adult white-tailed (*Odocoileus virginianus*) and mule deer (*O. hemionus*) to the distress signals of other mammal species. Both deer species only respond to distress signals from other species when they lie witin the range of pitches exhibited by their own species (Lingle & Riede, 2014; Teichroeb et al., 2013). Similarly, a honeyguide may need to mimic the pitch, and possibly also the temporal structure, of their primary host, in order to ensure that NLP is effective at manipulating provisioning rate.

Therefore, in this chapter I test the hypothesis that greater and lesser honeyguides exploit a sensory bias in their host parents to provision at a higher rate when there is more NLP present in the begging calls. First, I tested the prediction that honeyguides should have more NLP in their begging calls than do their respective hosts. To do so, I first compared measurements of acoustic variables associated with the presence of NLP between each honeyguide species, and both broods and single nestlings of their respective primary hosts. I separated begging calls from host broods and single host nestlings, since nestlings in a brood may have more NLP due to needing to compete with other nestlings, and therefore being more likely to dishonestly signal more than they need (Caro, West & Griffin, 2016). By separately comparing honeyguides to host broods and single nestlings, I can also assess whether there is evidence that honeyguides specifically mimic the NLP of a nestling in a brood as a potential mechanism for increasing provisioning, rather than just exploiting the host parents' generalised response to NLP. Second, I tested the prediction that host provisioning rates should be higher when begging calls with NLP features of a honeyguide are played back. I specifically tested the effect of amplitude modulation (one type of NLP) on provisioning rate by black-collared barbets. To do so, I conducted a playback experiment at black-collared barbet nests in which I manipulated black-collared barbet begging call recordings to match the amplitude envelope (smoothed changes in amplitude over time) of lesser honeyguide begging call recordings, and vice versa. If features of the lesser honeyguide amplitude envelope increase provisioning by barbet parents, then barbet begging calls with the amplitude envelope of the lesser honeyguide, and control lesser honeyguide begging calls with unmanipulated amplitude envelopes, should have similar provisioning rates. Furthermore, provisioning rates in response to these playbacks should be higher than those to playbacks of lesser honeyguide begging calls with the amplitude envelope of barbet begging calls, and to playbacks of control barbet begging calls.

3.3 Methods

3.3.2 Collection of begging call recordings

The same recordings used in Chapter 2 were used for this chapter. Recordings used for correlational analyses (Section 3.3.3) and playback experiment (Section 3.3.4) were made by Claire Spottiswoode (2008–2011) and Luke McClean (2016–2018). The correlational analyses were supplemented by recordings from Jess Lund (2021–2023) and myself (2022). For details of how the recordings were collected, see Section 2.3.1.

3.3.3 Correlational analyses of variables associated with NLP

3.3.3.1 Recording preparation

I only used stage 3 recordings in the analyses (zee Section 2.3.2 for an explanation of how development stages of begging calls were classified). Recordings contained between 1 and 19 begging bouts, with bouts typically being triggered by the arrival of a host parent. I extracted a 5 second clip from the beginning of each begging bout within each recording. I applied a high pass filter at 700 Hz cutoff frequency with a 24 dB rolloff to each clip. I decided on this cutoff level by examining spectrograms of each clip to determine the lower limits of pitch across recordings. I normalised the maximum amplitude of each clip to -3 dB to ensure recordings were at comparable amplitudes.

3.3.3.2 Measurement of variables associate with NLP

I used the function *analyze* in the *soundgen* package (Anikin, 2019) in R to make measurements of variables associated with NLP in all of the begging call recordings. The pitch floor was set to 700 Hz, and the pitch ceiling was set to 15 kHz, with a 2 kHz prior set for the pitch tracking. I measured the following variables: Wiener entropy, spectral novelty, feature-based flux, amplitude envelope frequency, amplitude envelope depth, roughness, subharmonics depth and subharmonics ratio. Each of these variables is associated with a different type of NLP (summarised in Table 3.2).

Table 3.2: Definitions of all the variables measured using *soundgen* (Anikin, 2019) that are associated with the presence of non-linear vocal phenomena.

Variable	NLP associated with this variable	Definition
Wiener entropy	Deterministic chaos	A measure of the randomness of an acoustic signal from 0–1, with 1 representing white

		noise and 0 representing pure tonal sound.
Amplitude modulation depth	Amplitude modulation	Depth of amplitude modulation estimated from a smoothed amplitude envelope from 0–1.
Amplitude modulation frequency	Amplitude modulation	Frequency of amplitude modulation estimated from a smoothed amplitude envelope.
Perceived roughness	Amplitude modulation	The amount of spectrotemporal modulation in the “roughness” zone of AM frequencies (30–150 Hz), estimated using a modulation spectrum.
Feature-based flux	Bifurcations	The rate of change in normalised acoustic features, which includes all features measured by *analyze* (Anikin, 2019).
Spectral novelty	Pitch jumps	A measure of how variable the spectrum is.
Subharmonic depth	Subharmonics	Estimated depth of subharmonics from 0–1, with 0 indicating no subharmonics, and 1 indicating subharmonics that are as strong as the fundamental frequency.
Subharmonic ratio	Subharmonics	The ratio of the fundamental frequency to the subharmonics frequency.

3.3.3.3 Statistical analysis

I assessed differences between each honeyguide and its host brood and single host nestling across all NLP types using principal component analysis (PCA). A PCA was conducted for each parasite-host system (greater honeyguides/little bee-eaters, and lesser honeyguides/black-collared barbets), and was informed by each of the variables associated with NLP (calculated in Section 3.3.4.2 above). All variables were scaled and centred. PCAs were implemented using the *prcomp* function in the *stats* package (R Core Team, 2023). The first two principal components of each PCA were visualised with a biplot created using *ggbiplot* (Vu, 2011).

For each parasite-host system, I also ran linear mixed-effects models (LMMs) to test for differences between each category (honeyguide, host brood, host single) in each individual variable associated with NLP. LMMs had each variable associated with NLP as a response, and recording identity nested within nest identity as a random effect. I implemented the LMMs using the *lmer* function in the package *lme4* (Bates et al., 2015). For each response variable, I ran models with and without category (honeyguide, host brood, host single) as a fixed factor. I compared models with category (test models) and those without category (null models) using corrected Akaike's Information Criterion (AICc) model selection implemented using the *AICc* function in *MuMIn* (Bartoń, 2022). I used this to assess whether adding category significantly improved model fit, and thus whether there is evidence for differences between the categories. I assessed homoscedasticity and normality of the residuals using residual and quantile-quantile plots created using *mcp.fnc* in the *LMERConvenienceFunctions* (Tremblay & Ransijn, 2020) package. If there were issues with convergence or a near singular model fit, I removed recording identity from the random effects structure and ran 100 iterations of model pairs with one random clip from each recording selected per iteration to prevent pseudoreplication. Where there was evidence for a difference between at least two categories (based on whether the test model was the best fitting, or whether a large proportion of iterations in which the test model was the best fitting), I ran Post-hoc Tukey Significance Tests to compare the estimated marginal mean for each response variable between categories. To do this, I used the *pairs* function in the *emmeans* (Lenth, 2023) package.

3.3.4 Playback experiment

To determine which variables to manipulate in the playback experiments, I conducted preliminary analyses using the same methods as the correlational analysis above (Section 3.3.3.3). The preliminary analysis was done using only a subset of the data, since some of the data had not yet been collected. This included only the data collected in 2008–2011 by Claire Spottiswoode and in 2016–2018 by Luke McClean. Based on the results for this subset, I found the strongest evidence for a difference between honeyguides and host begging calls in measures associated with the amplitude envelope (i.e. amplitude modulation frequency and roughness). Therefore, I manipulated the amplitude envelope in begging calls recordings of lesser honeyguides and black-collared barbet single nestlings, to create playback treatments for a playback experiment. The playback experiment was only conducted at black-collared barbet nests since the breeding period of little bee-eaters was much shorter than usual in the year that I conducted the experiments. This was likely due to a late start to breeding because of the late rains of the previous season, and finishing early because of the early rains experienced while I was in the field. The length of the breeding period in black-collared barbets was less affected. However, towards the end of the season, some of the dead branches with barbet nests became waterlogged and the branches broke at the weak point created by the nest cavity within the branch. Hence, I only tested the black-collared barbet–lesser honeyguide system.

3.3.4.1 Creating treatment clips

To test whether the amplitude envelope of the honeyguide begging calls elicits a higher provisioning rate from host parents, I swapped the amplitude envelopes of recordings of begging calls from single black-collared barbet and lesser honeyguide nestlings, to create playbacks for use in field experiments. The amplitude envelope is the smoothed change in the amplitude of the sound wave over time. Regular changes in the amplitude of a sound over time is called amplitude modulation and complex amplitude envelopes can be represented as a sum of various amplitude modulation frequencies. This is analogous to how complex sounds can be reduced to their component frequencies represented in a spectrogram.

I manipulated the amplitude envelopes of recordings by passing them through code within a custom Python (Van Rossum & Drake, 2009) script written by Emmanouela Rantsiou (2021). Two random 10 second clips were selected, one from a lesser honeyguide and another from a single black-collared barbet nestling. Each clip was filtered into 8 frequency banks between 1.5 Hz and 17 kHz. These were 8 clips made from the same clip, each with a different, non-overlapping frequency band of equal breadth.

The next steps were applied to each frequency bank independently. The component amplitude modulation (AM) frequencies between 11.5 Hz and 28 Hz were removed using a Butterworth bandstop filter. This range of AM frequencies was decided on since it represented the 10th and 90th percentiles of AM frequency in both lesser honeyguide and black-collared barbet recordings used in the preliminary analyses. The difference between the amplitude envelopes of the filtered and original clips was calculated to determine what component of the amplitude envelope was removed during the bandstop filtering. This component was then implanted into the envelope of the corresponding frequency bank of the bandstop filtered clip of the other species. The ratios between the filtered and implanted amplitude envelope and original amplitude envelope were then calculated, and the original audio signal for each frequency bank multiplied by this ratio, so that the amplitude envelope of each frequency bank was the same as the corresponding frequency bank of the other species. After each of these steps, each of the multiplied frequency banks were then summed together to create the manipulated clip with the amplitude envelope of the other species.

Control clips of each species were also created, whereby each step above was conducted, but instead of implanting the amplitude envelope of the other species, the amplitude envelope of the same clip was added back in. This was done to control for the effect of the manipulation on the clips.

For all clips, a lowpass filter at 17 kHZ was applied to remove artefacts visible as a vertical line on the spectrogram, and extends to very high frequencies. A Butterworth bandstop filter was also applied to the first bank (from 1.5–1063.9 Hz) to remove metallic sounding artefacts at lower frequencies than the bird vocalisations that are present as a result of the bank filtering. This created four treatments for the playback experiment:

(i) Host, modified: black-collared barbet begging call with AM frequencies of lesser honeyguide implanted.
(ii) Parasite, modified: lesser honeyguide begging call with AM frequencies of black-collared barbet implanted.
(iii) Host, control: black-collared barbet begging call with AM frequencies removed and reimplanted.
(iv) Parasite, control: lesser honeyguide begging call with AM frequencies removed and reimplanted.

3.3.4.2 Conducting playbacks

The protocol used for playback experiments at black-collared barbets followed McClean (2020). Nests of black-collared barbets with nestlings that had erupted pin feathers (approximately 10–15 days old) were used for experimental trials. This ensured that the nestlings did not require brooding by their parents and could spend periods outside of the nest. Prior to an experimental trial, all except one of the barbet nestlings was removed from the nest and placed in a container lined with leaves and grass. A JBL Clip 4 Bluetooth speaker (JBL Corporation, Los Angeles, USA) was attached to the outside of the nest, and hidden using broken pieces of bark, which were attached with thin malleable wire. The speaker was connected to an iPhone (Apple, Cupertino, USA) with the recordings that had undergone processing for each treatment. The maximum amplitude level was adjusted to be in the 55–65 dB range at 10 cm using a Cadrim digital sound level meter (Cadrim, Shenzhen, China). This level was used because it is comparable to the maximum amplitude of a brood of host nestlings, which was measured at 10 cm (McClean, 2020).

To count the number of visits to the nest by the parents and to initiate playbacks, I observed the nest while hidden within a bag hide 10–30 meters from the nest. Each time a black-collared barbet entered the nest, I played one of the 10 second playback clips. Each nest received playbacks created from a different original barbet or lesser honeyguide recording. Barbets were allowed to visit the nest three times, to allow them to acclimatise to the set up, and to give each parent the opportunity to hear the clip. After this, I recorded the number of times a parent visited the nest in the next hour. I counted each time an adult barbet entered the nest as a visit. Each time they did, I again played the playback clip. McClean (2020) demonstrated using cameras within the nest that adult black-collared barbets fed nestlings on each visit to the nest, and so the rate of visits to the nest was assumed to equal the provisioning rate. Each barbet nest was visited on four consecutive days, with a different treatment used as the playback on each day. The order of the treatments was randomised for each barbet nest. Fortunately, none of the nests was predated before the completion of each set of treatments.

3.3.4.3 Statistical analysis

To test whether there was a difference in provisioning rate between treatments, I ran an LMM with the provisioning rate as the response, nest identity as a random factor, and the treatment and the ordinal day (day 1, 2, 3 or 4) as fixed factors. The following planned contrasts (Ruxton & Beauchamp, 2008; Schad & Kliegl, 2020) between the treatments were specified a priori:

(i) Host modified and parasite control compared to parasite modified and host control.
(ii) Host modified compared to parasite control.
(iii) Parasite modified compared to host control.

The LMMs were implemented using the *lmer* function in the *lme4* package. I assessed homoscedasticity and normality of the residuals using residual and quantile-quantile plots created using *mcp.fnc* in the *LMERConvenienceFunctions* (Tremblay & Ransijn, 2020) package. Z-tests from the model output were used to determine whether there is a significant difference in provisioning rate for each contrast.

To determine whether amplitude modulation and roughness differed between treatments, and thus whether the manipulation affected these variables in the intended manner, I performed a repeated-measures analysis of variance (ANOVA) on the clips used in the experiments using the *aov* function in the *stats* package (R Core Team, 2023). If the results of the ANOVA suggested a difference between at least two treatments, post-hoc Tukey Significance Tests were performed to determine which treatments differ from each other. This was implemented using the *pairs* function in the package *emmeans* (Lenth, 2023).

3.4 Results

3.4.1 Do honeyguides display more NLP than their hosts?

A total of 129 stage 3 recordings were used in the correlational analyses. These were taken from 31 unparasitised black-collared barbet broods (32 full brood recordings, comprising 2–4 chicks, and 9 recordings of single nestlings), 12 lesser honeyguide chicks in black-collared barbet nests (13 recordings), 20 unparasitised little bee-eater broods (15 full brood recordings, comprising 2–5 chicks, and 10 recordings of single nestlings), and 20 greater honeyguides in little bee-eater nests (50 recordings). I took clips from the beginning of each of the 532 begging bouts recorded.

Biplots of the first two principal components of the PCA suggest that greater honeyguides have generally lower values for PC1 than bee-eater broods and singles (Figure 3.1A). The highest absolute values for the loadings on PC1 were from amplitude modulation depth, perceived roughness, and spectral novelty, each of which had a negative loading (Appendix, Table S3.1). This suggests that greater honeyguides may have greater amplitude modulation depth, roughness, and spectral novelty than bee-eater brood and single bee-eater nestlings.

In contrast, biplots of the first two principal components of the PCA suggest lesser honeyguides do not appear to differ from either barbet broods or single nestlings in PC1 or PC2 (Figure 3.1B). However, barbet broods appear to have a lower value for PC1 than single barbet nestlings. The variables with the highest absolute loadings on PC1 for the lesser honeyguide and barbets were feature-based flux, amplitude modulation depth and perceived roughness. Amplitude modulation depth had a positive loading, whereas flux and roughness also had negative loadings (Appendix, Table S3.2). This suggests that barbet broods have higher roughness and flux than single barbet nestlings.

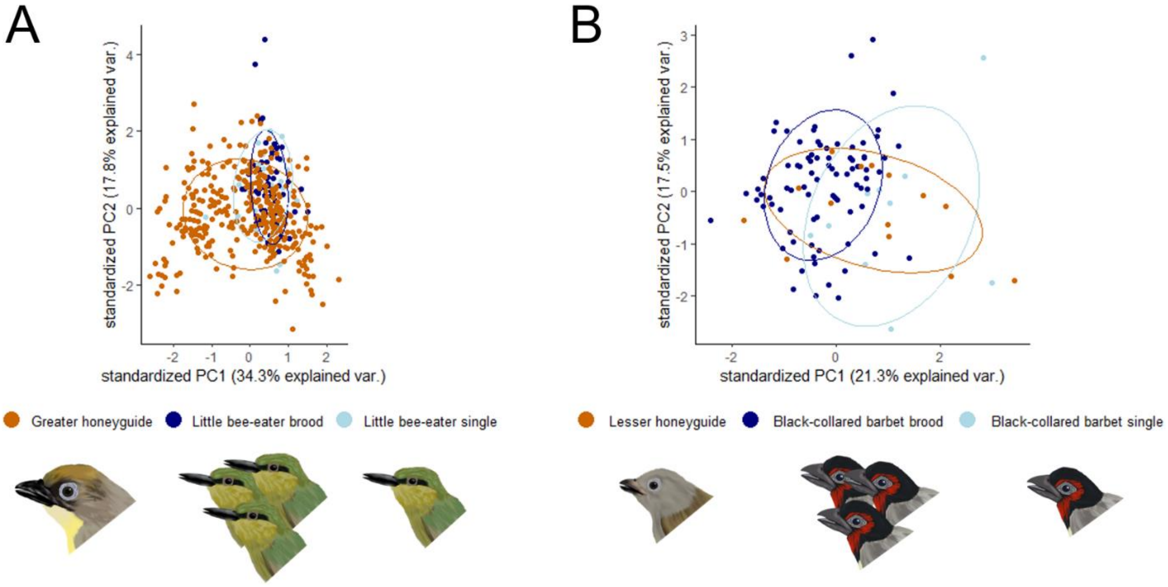


Figure 3.1: Biplots of first two principal components of variables associated with NLP for each parasite-host pair: (A) greater honeyguides and little bee-eaters, and (B) lesser honeyguides and black-collared barbets. Each dot represents a different clip and the colour indicates the category of the clip (honeyguide, host brood or host single).

Two approaches were taken for the LMMs, since the models for some of the response variables resulted in singular fit or failed convergence. In these cases, recording identity was dropped as a random factor, and 100 iterations of model pairs (models with and without species identity as a fixed factor) were run, with a randomly selected clip taken from each recording to avoid pseudoreplication.

There was no evidence for a difference between greater honeyguide, little bee-eater brood and little bee-eater single begging calls in any variables related to NLP, except for amplitude modulation frequency. For amplitude modulation frequency, in 100% of the iterations the model with category included as a fixed factor fitted significantly better than the model without a fixed factor. Little bee-eater broods wa significantly higher than greater honeyguides in their estimated marginal means in 38% of iterations. However, bee-eater broods were only significantly higher than single bee-eater nestlings in 10% of iterations. In none of the iterations were greater honeyguides significantly different from single bee-eater nestlings. Greater honeyguide begging calls are thus consistently lower in amplitude modulation frequency than little bee-eater broods, and more similar to single little bee-eater nestlings than to little bee-eater broods. Roughness was the only other variable where there was some evidence for a difference between categories, since the model with category as a fixed factor fitted better than the model without it. However, the difference in fit was not substantial (ΔAICc < 2). In summary, bee-eater broods had a higher amplitude modulation than single bee-eaters and greater honeyguides, which were similar to each other, and in each of the other variables there was no difference between single bee-eaters, bee-eater broods and greater honeyguides.

Table 3.3: Results of AICc-based model selection on the LMMs with response variables associated with NLP that had neither a singular model fit nor convergence issues when recording identity was included in the random effects structure. “Null” refers to the model without category (greater honeyguide, little bee-eater brood or little bee-eater single), and “test” refers to the model with category as a fixed effect. ΔAICc > 2 was considered significant.

Variable	Best fitting model	ΔAICc
Amplitude modulation depth	Null	8.56
Wiener entropy	Null	4.95
Roughness	Test	1.32
Spectral novelty	Null	10.25
Subharmonic ratio	Null	8.14

Table 3.4: Results of AICc-based model selection on the LMMs with response variables associated with NLP that had a singular model fit or convergence when recording identity was included in the random effects structure. I present the number of iterations out of 100 where the model with category (greater honeyguide, little bee-eater brood or little bee-eater single) included as a fixed factor (test model) was significantly better fitting than the model without category (null model). ΔAICc > 2 was considered significant.

Variable	# iterations where test model fit better than null model (ΔAICc > 2, 100 iterations)
Amplitude modulation frequency	100
Feature-based flux	0
Subharmonic depth	0

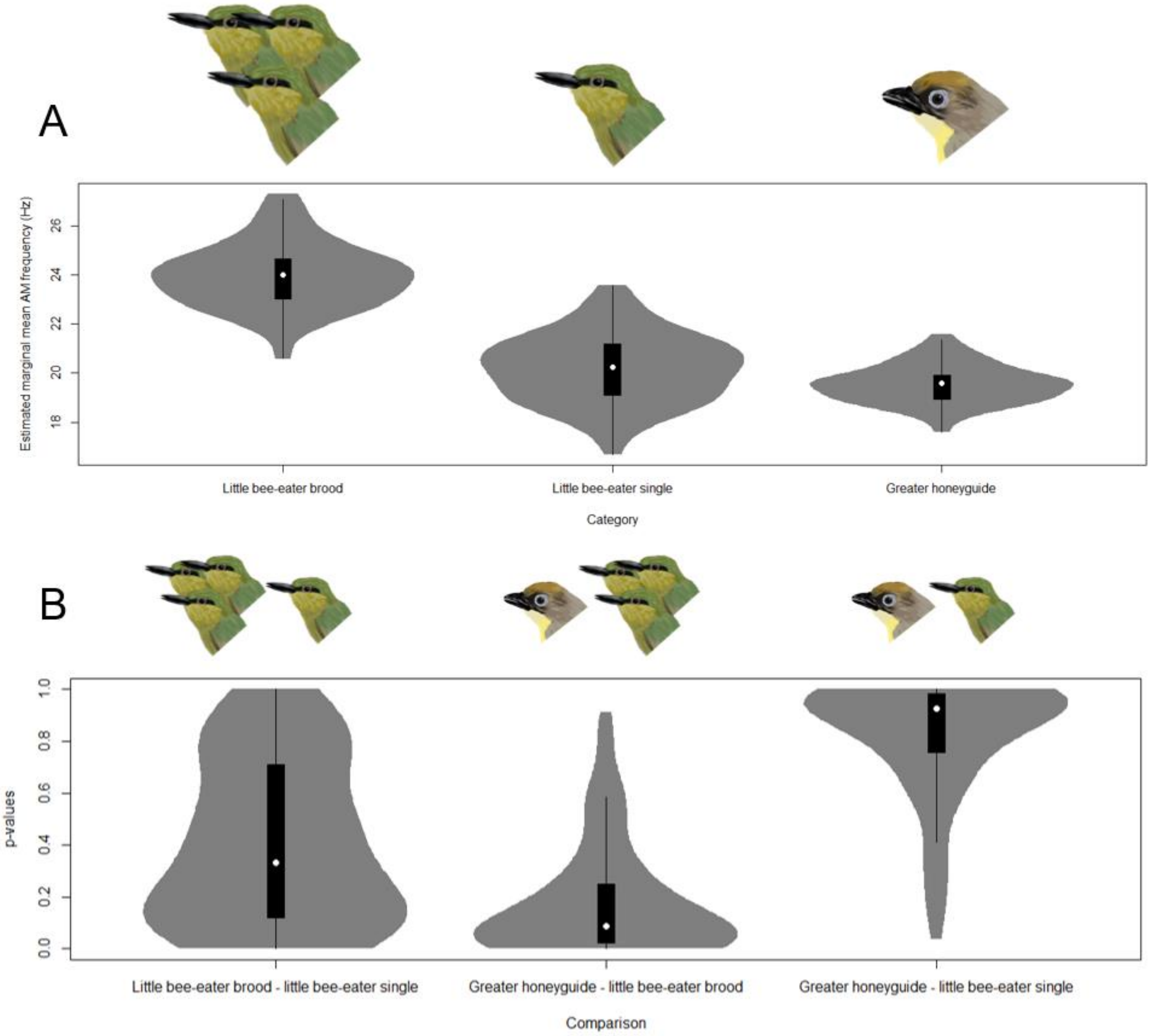


Figure 3.2: Little bee-eater broods tended towards higher amplitude modulation frequency than single bee-eater nestlings and greater honeyguides. However, the difference was only significant in most iterations between bee-eater broods and greater honeyguides. Violin plots of (A) estimated marginal means of AM frequency, and (B) *p*-values of the Tukey significance tests for each pairwise comparison between categories from 100 iterations of LMMs.

For the black-collared barbet and lesser honeyguide recordings, the two variables related to NLP that had the most evidence of a difference between the categories were amplitude modulation frequency and roughness (Table 3.6). Both variables measure features related to the amplitude envelope of the calls. Lesser honeyguides had a higher average amplitude modulation frequency (Figure 3.3B) but this was only significantly different from the black-collared barbet broods and single nestlings in 1% and 7% of the iterations respectively (Figure 3.3A). Black-collared barbet broods had a significantly higher perceived roughness than single black-collared barbet nestlings in 38% of the iterations. Lesser honeyguides had on average higher perceived roughness than single black-collared barbet nestlings, but only differed significantly from black-collared barbet broods and single nestlings in 11% and 12% of the iterations respectively. In each of the other variables associated with NLP, there was no evidence for a difference between the categories, either because the model without category as a fixed factor had a better fit (Table 3.5) or, in models with convergence issues or singularity, because the model without category as a fixed factor had a better fit in almost all of the iterations (Table 3.6). In summary, both single lesser honeyguides and black-collared barbet broods had higher values for variables associated with amplitude modulation, particularly perceived roughness, than single barbet nestlings, but not in any of the other variables.

Similarly to the preliminary analyses with limited data, these results suggest that features related to the amplitude envelope of lesser honeyguide begging calls may be responsible for manipulating the provisioning of barbets. This retrospectively supported the prior decision to manipulate this feature in the playback experiment.

Table 3.5: Results of AICc-based model selection on the LMMs with response variables associated with NLP that had neither a singular model fit nor convergence issues when recording identity was included in the random effects structure. “Null” refers to the model without category (lesser honeyguide, black-collared barbet brood or black-collared barbet single), and “test” refers to the model with category as a fixed effect. ΔAICc > 2 was considered significant.

Variable	**Best fitting model**	**ΔAICc**
Wiener entropy	Null	7.41
Subharmonic depth	Null	17.36

Table 3.6: Results of AICc-based model selection on the LMMs with response variables associated with NLP that had a singular model fit or convergence issues when recording identity was included in the random effects structure. I present the number of iterations out of 100 where the model with category (lesser honeyguide, black-collared barbet brood or black-collared barbet single) included as a fixed factor (test model) was significantly better fitting than the model without category (null model). ΔAICc > 2 was considered significant.

Variable	**# iterations where test model fit better than null model (ΔAICc > 2, 100 iterations)**
Amplitude modulation depth	2
Amplitude modulation frequency	55
Roughness	81
Feature-based flux	0

Spectral novelty	0
Subharmonic ratio	42

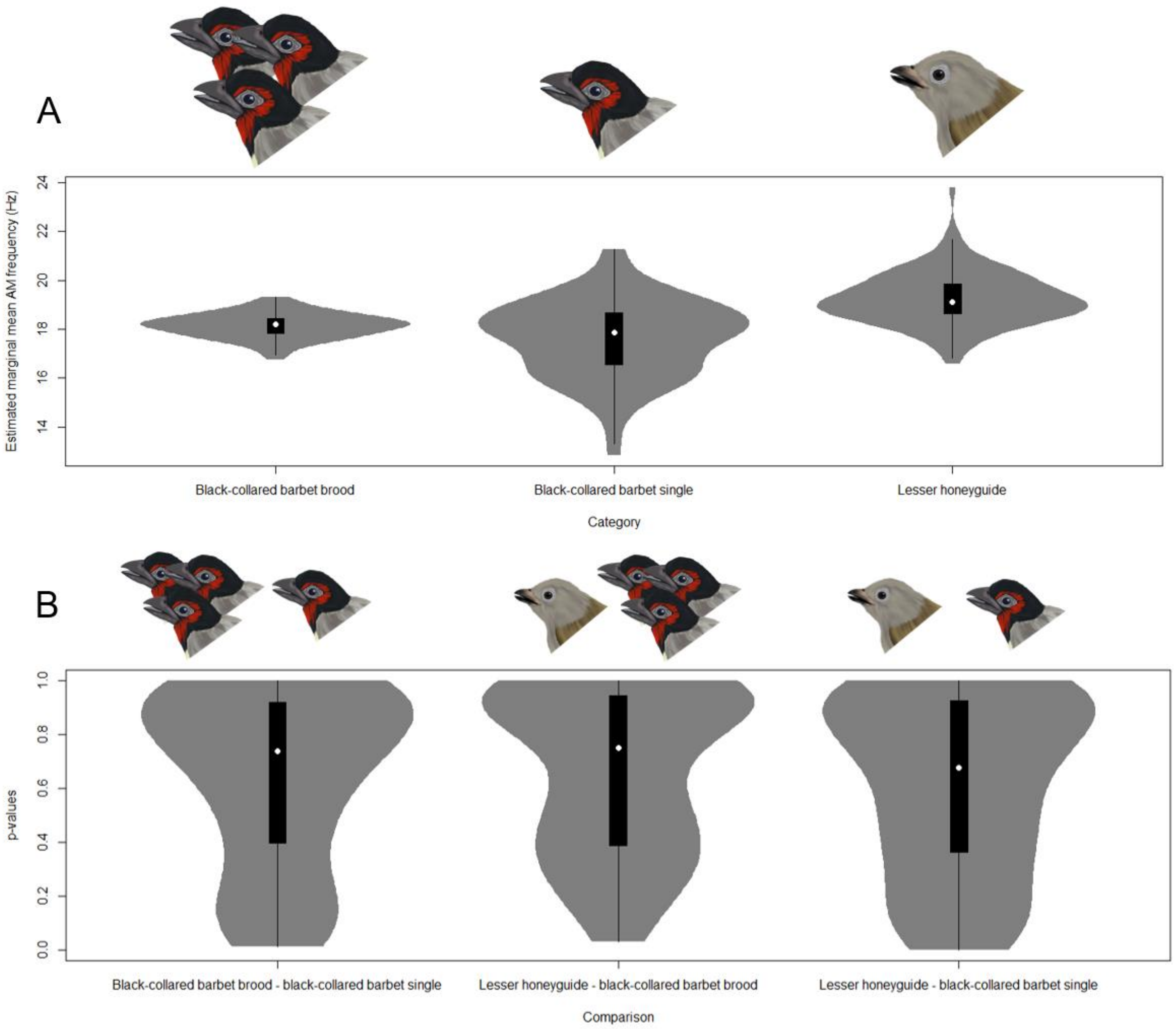


Figure 3.3: Lesser honeyguides tended towards higher amplitude modulation frequency than black-collared barbet broods and single nestlings, but this was not significant in most model iterations. Violin plots of (A) estimated marginal means of amplitude modulation frequency, and (B) *p*-values of the Tukey significance tests for each pairwise comparison between categories from 100 iterations of LMMs.

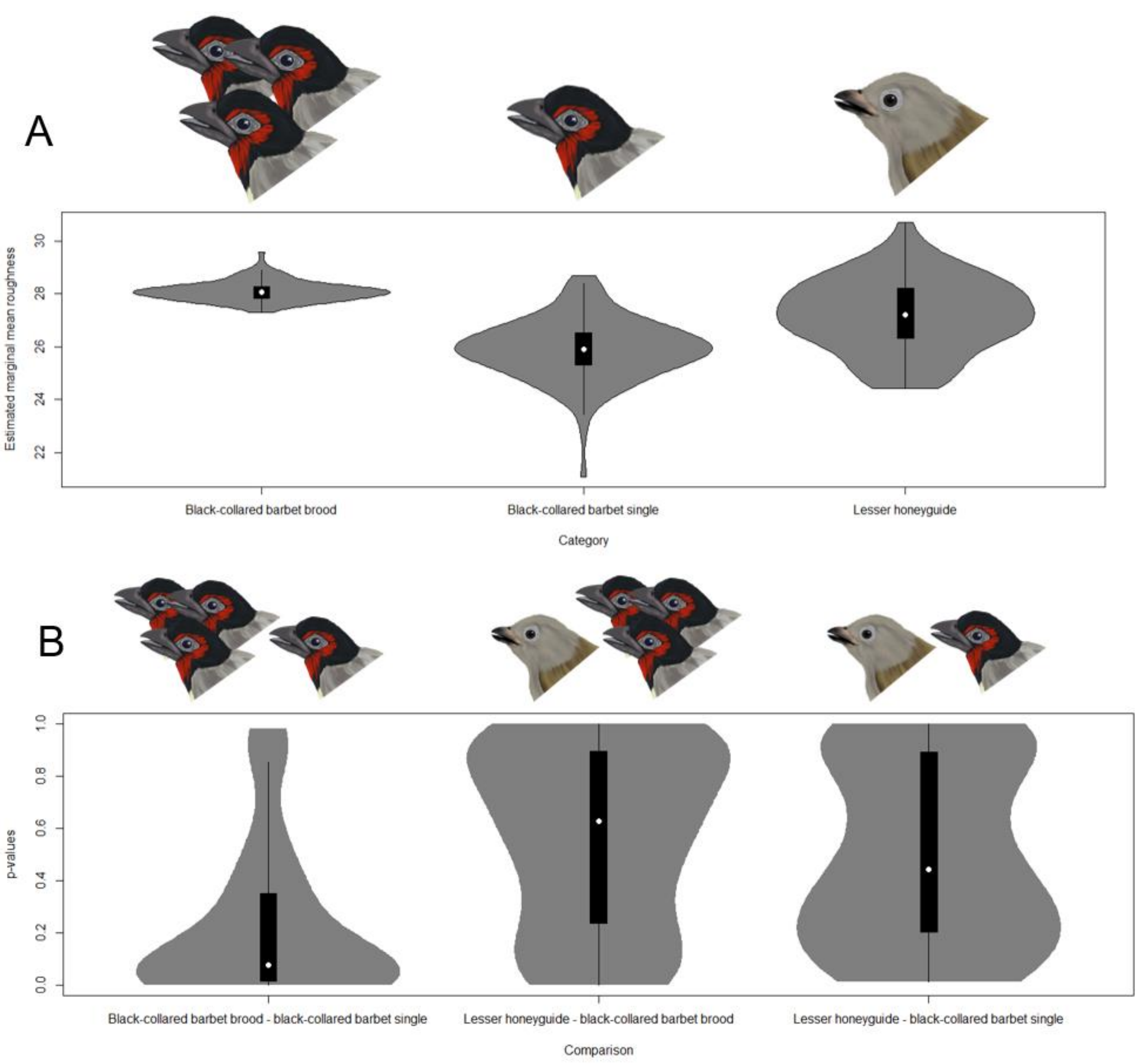


Figure 3.4: Black-collared barbet broods and lesser honeyguides tended towards higher perceived roughness than single barbet nestlings. However, the difference was only significant in most iterations in barbet broods and single nestlings. Violin plots of (A) estimated marginal means of perceived roughness, and (B) *p*-values of the Tukey significance tests for each pairwise comparison between categories from 100 iterations of LMMs.

3.4.2 Playback experiment

I conducted eight playback trials, with each of the four treatments (host, modified; host, control; parasite, modified; parasite, control) played once per trial in a randomised order. The best-fitting model included treatment and ordinal day as fixed factors, and was significantly better-fitting than a null model without any fixed factors (ΔAIC = 8.17), and than a model with only treatment included as a fixed factor (ΔAIC = 4.60). All models included nest identity as a random factor. This model was therefore used for the comparisons between treatments.

I found that barbet adults did not provision at a faster rate when played modified host and parasite control recordings than when they were played host control and modified parasite recordings ($\beta = 2.50$, $t_{18} = 1.360$, *p*-value = 0.190). There was also no significant difference in response to modified host and parasite control recordings ($\beta = 1.42$, $t_{18} = 0.537$, *p*-value = 0.598), nor in response to host control and modified parasite recordings ($\beta = 4.73$, $t_{18} = 1.448$, *p*-value = 0.165). Thus, it appears that the amplitude envelope of the lesser honeyguide's call did not affect the provisioning rate of the host parents, at least at a level detectable by the sample size of the experiments and in the range of AM frequencies manipulated.

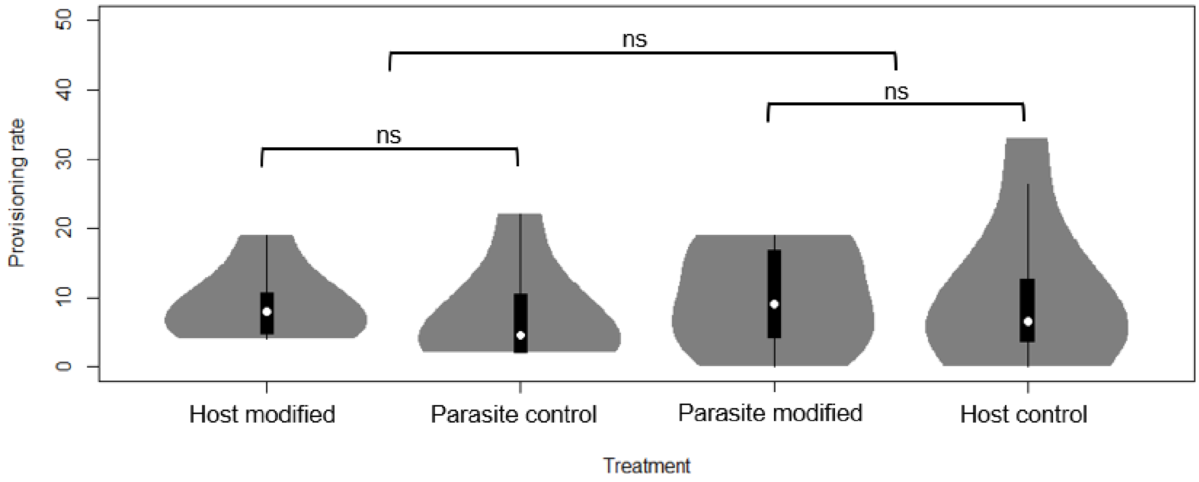


Figure 3.5: Violin plots showing the distribution of provisioning rates (black-collared barbet nest visits per hour) for each treatment. Each of the "modified" treatments had the amplitude envelope of the other species between the AM frequencies of 11.5–28 Hz. "Control" treatments did not have the amplitude envelopes swapped but had undergone each of the other processing steps to control for the effects of the processing on the recordings. "Parasite" refers to lesser honeyguide begging call recordings, and "host" refers to single black-collared barbet begging call recordings. The significance level for each planned contrast is indicated. None of the contrasts was significant.

The roughness and amplitude modulation frequency of the clips used in each treatment was measured to determine how the experimental manipulation affected these variables using the same metrics applied to the correlational analyses. There was a trend for mean roughness to be higher in the modified host and parasite control compared to the modified parasite and host control clips, but this was not significant (*F* = 0.85, *df* = 3, *p*-value = 0.48). However, amplitude modulation frequency was significantly higher in the host modified treatment than any other treatment, and host control significantly lower than the other treatments. Parasite modified and parasite control were intermediate and did not differ from each other (Appendix: Table S3.4). Therefore, the manipulation of the begging calls only significantly affected AM frequency in host begging calls, and not in parasite begging calls.

3.5 Discussion

In this chapter I tested the hypothesis that honeyguides use NLP in their begging calls, to increase provisioning by their host parents to levels exceeding those provided to the host's own nestlings. This could arise either because host parents associate NLP with more nestlings that need to be fed, and/or because host parents have a sensory bias that favours an elevated response to NLP. I found no strong evidence that honeyguides use NLP to increase host provisioning: first, the correlational analyses showed that neither greater nor lesser honeyguides had significantly higher values for variables associated with the presence of NLP than did single host nestlings. This is inconsistent with the hypothesis that honeyguides use NLP to manipulate the provisioning rate of their host parents. However, amplitude modulation frequency and roughness were higher in begging calls from host broods than single nestlings. This suggests that NLP is a plausible cue that host parents may use to assess how many nestlings need to be fed. Second, the playback experiment suggested that the amplitude envelope between the AM frequencies 11.5 Hz and 28 Hz did not affect provisioning by black-collared barbets. However, this experiment cannot reveal anything conclusive about the amplitude envelope as a whole and so cannot fully exclude the possibility that NLP in general, or amplitude modulation in particular, may affect host provisioning.

Despite the absence of clear evidence that honeyguides use NLP to increase the provisioning by their primary hosts, it remains possible that honeyguides do use NLP, but not at levels detectable by these analyses. For example, it is possible that NLP is only present in short time periods within the recordings, and that during most spectrogram frames the honeyguides are similar to hosts. In order to exclude this, entire spectrograms need to be inspected for evidence of NLP, and their nature and frequency compared to those of host begging calls. Alternatively, the absence of any detectible clear difference between honeyguides and their hosts may reflect a real absence of difference. Perhaps honeyguides cannot significantly exceed the quantity of NLP present in host begging calls, since it may then undermine host mimicry and provide a cue to host parents that the nest has been parasitised, leading to chick rejection (Holen et al., 2001). There may also be selection against elevated NLP, if the begging call becomes altered to a point that it is no longer recognised as a begging signal by the host parent.

3.5.1 Roughness in black-collared barbet and lesser honeyguide begging calls

Black-collared barbet broods had significantly higher perceived roughness than single black-collared barbet nestlings. Perceived roughness is calculated by assessing the amplitude modulation within the "roughness frequency range" of AM frequencies (30–150 Hz) (Anikin, 2019) using a modulation spectrum. Lesser honeyguides had a wide range of roughness values that overlapped with those of both single barbet nestlings and barbet broods: lesser honeyguides appeared to exhibit higher levels of roughness than single barbet nestlings some of the time, but similar levels at other times. Thus, it may be possible that lesser honeyguides did not maintain the same high levels of roughness as those of host broods, but by exhibiting high roughness some of the time they may still be able to increase provisioning rates of barbet parents. The playback experiments did not effectively test the effect of roughness on host parents since the clips from different treatments were not significantly different in perceived roughness.

The fact that multiple black-collared barbet nestlings in a brood call simultaneously may influence their perceived roughness. Specifically, the elevated roughness of recordings of barbet broods may result from interference between the amplitude envelopes of each individual barbet, leading to a more complex envelope structure with high frequency amplitude modulation (Espinosa, 2017). Interference beats, which cause sinusoidal amplitude modulation when sounds of two slightly different pitches interfere, may also occur when nestlings beg simultaneously, and their calls are at slightly different pitches. This may introduce further amplitude modulation frequencies (Espinosa, 2017). High frequency amplitude modulation may therefore act as a cue to barbet parents of the number of nestlings present. Therefore, by exhibiting high frequency amplitude modulation, even if only some of the time, lesser honeyguides may elicit the same provisioning response from barbet parents as a brood of host nestlings. Alternatively, roughness in the begging calls of individual chicks may be higher in broods than single nestlings because competition between nestlings increases when more nestlings are present in the nest (Ricklefs, 2002). However, there may be a cost associated with increased roughness, such as an increased detectability to predators. This may select for roughness only to be exhibited some of the time, if it still leads to an elevated provisioning response by barbet parents (Haskell, 2002). In summary, perceived roughness may be a cue that barbet parents use to assess how many nestlings require feeding, and by exhibiting similar levels of roughness some of the time, lesser honeyguides could possibly use this cue to manipulate the barbets' provisioning.

3.5.2 AM frequency of greater honeyguide and little bee-eater begging calls

There was strong evidence that little bee-eater broods had a higher AM frequency than greater honeyguides, and some evidence that AM frequency was also higher in bee-eater broods than in single bee-eater nestlings. Since little bee-eater nestlings in a brood do not call simultaneously most of the time, the observed higher AM frequency in bee-eater broods is not the result of interference between nestling begging calls. AM frequency may therefore be a signal of need in the begging calls of bee-eater nestlings, and AM frequency may be consistently higher in bee-eater broods if nestlings respond to competition with nestmates by increasing their AM frequency (Ricklefs, 2002). Sensitivity to AM has been demonstrated in budgerigars (*Melopsittacus undulatus*), zebra finches (*Taeniopygia guttata*) and common starlings (*Sturnus vulgaris*), and studies of the midbrain responses in these species suggest that they can detect AM up to a higher AM frequency threshold than humans, and with higher resolution (Dooling & Searcy, 1981; Henry et al., 2016; Langemann & Klump, 2001; Woolley & Casseday, 2005). Therefore, it is plausible that the hosts of each honeyguide species is sensitive to the differences in AM frequencies in the begging calls of broods and single nestlings. However, even if this is the case, it does not appear that greater honeyguides use AM frequency to affect host provisioning.

3.5.3 Higher provisioning to honeyguides than hosts was not replicated

I found that control lesser honeyguide begging calls did not elicit higher provisioning rates from barbet parents than the control begging calls of a single barbet chick. This is contrary to previous findings in a similar playback experiment at the same study site by McClean (2020). This is surprising since McClean (2020) found highly significant differences between honeyguide and single host begging call treatments. The sample size of the present study has 71.1% power to detect the same effect size as observed by McClean (2020). Even though this is not above the ideal 80% minimum power threshold (Suresh & Chandrashekara, 2012), this nonetheless implies a fair probability that this effect would have been detected had it been present. I suggest two possible reasons for the different result observed in this study. First, the control recordings used in my study did go through some modification, since their amplitude envelope was removed and recovered, to control for any side-effects of the manipulation of the other treatments. Perhaps an important feature affecting provisioning by host parents was removed during the process of removing and recovering the amplitude modulation. Second, it is possible that differences in food availability between years could account for the different findings. For example, in stitchbirds (*Notiomystis cincta*), when food was limited females did not adjust provisioning rate in response to nestling demand, whereas males always provisioned proportionally to nestling demand (Low, Makan & Castro, 2011). Similarly, if food is limited in a particular year, barbet parents may not be able to keep up with the demands of even a single nestling, and this may explain the similar provisioning rates across treatments in the playback experiment. Limited food availablity is plausible given the poor and erratic rainfall in the prior season.

3.5.4 NLP as a potential signalling feature in avian begging calls that can be exploited by brood parasites

The use of NLP for signalling in mammals has been well studied, whereas in birds it is relatively unexplored. For example, NLP in calls given to solicit parental care has been investigated in diverse mammals including humans, deer, crocodiles, chimpanzees, and bonobos (Lingle & Riede, 2014; Teichroeb et al., 2013; Thévenet et al., 2023). However, the presence of NLP in the begging calls of nestling birds and the use of NLP as a signal of need has not been studied prior to the present study. While the presence of NLP and mechanisms behind the production of NLP in birds has been examined (Digby et al., 2014; Fee et al., 1998), the functional role of NLP in bird vocalisations requires more study, especially in the context of begging. In this study I have suggested that NLP may offer a signalling mechanism that could be used when the pitch and temporal structure of the begging calls is constrained, for example by the need to be recognised as the correct species. Brood-parasitic birds may have to first ensure that they are recognised as the correct species, which may constrain how much they can alter pitch or temporal arrangement.

A possible constraint on the deployment of NLP in begging calls is that it could plausibly increase their conspicuousness or attractiveness to predators, just as mammalian begging calls with high NLP are more attractive to predators (Thévenet et al., 2023). Conversely, this could favour elevated NLP if it elevates parent provisioning following the blackmail hypothesis, which proposes that chicks "blackmail" their parents by making themselves vulnerable to predation through conspicuous signals, which are reduced when they become satiated (Thompson et al., 2013). The blackmail hypothesis is however probably not likely to apply in the host species examined in this study, since there is likely high residual reproductive value of adults and relatively low reproductive value of single clutches.

In both primary hosts examined in this study, host broods appeared to have higher amplitude modulation frequencies and perceived roughness than single host nestlings. Even if it is unclear whether honeyguides use these features to manipulate their host parents, this result demonstrates that NLP has the potential to be used to simulate cues associated with more nestlings that need to be fed. NLP therefore deserves investigation in other systems as a mechanism to facilitate brood mimicry and manipulate host parents.

Additionally, since NLP appears highly conserved across taxa as a signal of high arousal states (Thévenet et al., 2023), NLP may be useful to affect the provisioning of multiple species. If this is the case, using NLP to manipulate host parent provisioning may be particularly useful for a generalist brood parasite. Each of these points illustrate that the function of NLP for signalling in birds, and its potential exploitation by avian brood parasites, deserves further exploration.

3.5.5 Future directions

The effects of NLP on host provisioning can be tested with more playback experiments where features of NLP are manipulated. I recommend that future playback experiments use synthetically created recordings based on recordings of real signals, in which the quantity of NLP can be directly adjusted in the creation of the recordings, rather than swapping features between recordings taken of real nestlings. The former was shown to be effective in testing behavioural responses to NLP in other animals (Anikin et al., 2022), whereas I found that swapping features between recordings was only partially successful, since it is difficult to isolate precise features without artefacts being introduced which need to be mitigated by further processing. As a result, it is difficult to be sure of precisely what the host parents are responding to. Synthetic recordings would have allowed more precise manipulation of call features. However, creating synthetic playbacks presents different challenges. To create synthetic begging calls, real begging calls are recreated using synthetic models. The parameters of these models are adjusted using the human eye and ear, which does not necessarily accurately represent the perception by the avian host parents. These were my main considerations when I decided not to use this approach for the experiment in this study.

Further playback experiments could then be conducted on the lesser honeyguide – black-collared barbet system, and perhaps on the greater honeyguide – little bee-eater system, in which amplitude modulation frequency and roughness were more precisely manipulated. Additionally, analyses examining the presence of NLP in honeyguide begging calls in more detail, for example exploring how NLP changes through the course of a begging bout, may provide more evidence for whether NLP is likely being used exploitatively by honeyguides. Since provisioning is higher to honeyguides than to host nestlings (at least in some years), the mechanisms of this process are worth examining further. Perhaps it is worth exploring the potential for exploitation of NLP by other brood parasites. In great spotted cuckoos (*Clamator glandarius*), Bolopo et al. (2015) found an association between a subjective assessment of “begging intensity” to the human ear and provisioning of food to brood parasites by host parents. Perhaps in this system the intensity of the begging signals may be altered by the presence of NLP, providing one possible candidate for future study.

3.5.6 Conclusion

The results of this study are inconclusive as to whether NLP in begging calls could be used manipulatively by brood parasites. The begging calls of honeyguides did not contain more NLP than those of their hosts (despite host broods containing more NLP than single host chicks), and I did not find experimental evidence that NLP increases provisioning rate by black-collared barbets. Nevertheless, this study is the first investigation into the use of NLP in avian begging calls and sets a foundation for future work. Further studies examining different systems and using differently designed playback experiments are necessary to test whether NLP affects provisioning responses in birds, and so whether it may be exploited by brood parasites. Inconsistencies between the results of the present study and a previous playback experiment suggest that provisioning behaviour by black-collared barbets may vary depending on food availability in different years, which is important to consider when conducting playback experiments. Overall, the prevalence and use of NLP in avian begging calls warrants further investigation, and NLP may yet prove to provide a useful signalling mechanism particularly when there are constraints on the pitch or temporal structure of acoustic signals.

3.6 Appendix

Table S3.1: Loadings of the first two principal components (PC1 and PC2) on the variables associated with NLP for the little bee-eater and greater honeyguide recordings.

Variable	PC1	PC2
Wiener entropy	-0.121	0.502
Amplitude modulation depth	-0.535	-0.072
Amplitude modulation frequency	0.409	-0.004
Perceived roughness	-0.491	-0.179
Feature-based flux	-0.238	0.227
Spectral novelty	-0.465	-0.054
Subharmonic depth	0.019	0.720
Subharmonic ratio	0.133	-0.371

Table S3.2: Loadings of the first two principal components (PC1 and PC2) on the variables associated with NLP for the black-collared barbet and lesser honeyguide recordings.

Variable	PC1	PC2
Wiener entropy	0.139	-0.324
Amplitude modulation depth	0.435	0.441
Amplitude modulation frequency	-0.266	-0.599
Perceived roughness	-0.428	0.338
Feature-based flux	-0.488	0.058
Spectral novelty	-0.300	-0.055
Subharmonic depth	-0.302	-0.039
Subharmonic ratio	-0.344	0.468

Table S3.3: Results from post hoc contrasts between each of the treatments, averaged over ordinal day of treatment. Degrees of freedom estimated using

Kenward-Roger method and *p*-values adjusted using Tukey's method for comparing a family of 4 estimates.

Contrast	**Estimated difference in marginal means**	**Degrees of freedom**	***t*-value**	***p*-value**
Host-modified/Host control	4.158	18	1.485	0.4666
Host modified/Parasite modified	0.575	18	0.200	0.9971
Host modified/Parasite control	1.422	18	0.537	0.9489
Host control/Parasite control	4.733	18	1.448	0.4874
Parasite modified/Host control	5.580	18	2.005	0.2229
Parasite modified/Parasite control	0.847	18	0.311	0.9892

Table S3.4: Pairwise contrasts of estimated marginal mean amplitude envelope frequency for the clips used for the playback experiment treatments.

Contrast	**Estimate**	**SE**	**DF**	***t*-value**	**Adjusted *p*-value**
Host modified/Parasite control	12.844	2.24	25	5.739	<0.001
Host modified/Parasite modified	12.460	3.04	25	4.095	0.002
Host modified/Host control	21.812	4.03	25	5.413	<0.001
Parasite control/Parasite modified	-0.385	2.27	25	-0.169	0.998
Parasite control/Host control	8.967	3.04	25	2.953	0.032
Parasite modified/Host control	9.352	2.32	25	4.026	0.003

CHAPTER 4

Synthesis

In this dissertation, I aimed to investigate whether greater and lesser honeyguides (*Indicator indicator* and *I. minor*) mimic the nestling begging calls of their primary hosts, and how honeyguide nestlings are able to manipulate the provisioning rate of their host parents using acoustic signals. First, I tested whether there is evidence of begging call mimicry by honeyguides by comparing the begging calls of the two honeyguide species to those of one another and of their hosts. Next, I examined whether there is evidence of call rate, or any other feature describing the pitch and temporal structure of begging calls being used by honeyguides to manipulate the provisioning rate of their host parents through either brood mimicry or supernormal stimulus. Finally, I tested whether honeyguides may be using non-linear vocal phenomena, a feature that plausibly signals need in begging calls, but which has not been investigated before in this ecological context, as a supernormal stimulus to manipulate host parent provisioning.

4.1 Key findings

4.1.1 Primary host mimicry

I found quantitative support for primary host mimicry by both greater and lesser honeyguide since the begging calls of each honeyguide species were more similar to those of their primary host than to those of one another. Honeyguides appear to specifically match the pitch and temporal structure of host begging calls. Therefore, these may be important features that host parents use to recognise calls coming from their own chicks. This study adds to the growing number of quantitative assessments of mimicry in brood parasites, to support previous subjective assessments of begging call similarity between brood parasites and their hosts.

4.1.2 Host brood mimicry

I found no evidence that either honeyguide species mimics features of host broods, contrary to the suggestions of previous observers. Nestlings of the lesser honeyguide’s primary host, the black-collared barbet (*Lybius torquatus*), do beg simultaneously, and I therefore anticipated that features such as temporal and spectral entropy and call rates may be cues that host parents could use to assess the number of nestlings that need to be fed. I found that these features do appear to be useful to distinguish between host broods and single nestlings, but that lesser honeyguides do not appear to mimic these features of broods. By contrast, nestlings of the primary host of the greater honeyguide, the little bee-eater (*Merops pusillus*), typically do not beg simultaneously, and therefore any cues of a brood that may be available for mimicry by honeyguides would have to arise from the presence of nestmates altering the calls of individual nestlings. I found spectral and temporal entropy were again useful to distinguish between bee-eater broods and single nestlings, but again, lesser honeyguides did not mimic these features of broods. Therefore, another mechanism must be responsible for the increased provisioning to honeyguide nestlings by their host parents (McClean 2020). Call rate, which is the feature that has been shown to increase provisioning in other systems (Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2013; Kilner, Noble & Davies, 1999; Ursino et al., 2018), does not appear to be useful in this system to increase provisioning. In other systems, elevated call rates exhibited by brood parasites is likely the result of brood mimicry, since call rate is proportional to the number of nestlings needing food if they are begging simultaneously (Davies, Kilner & Noble, 1998; Gloag & Kacelnik, 2013). However, since honeyguides mimic the structure of individual nestling calls, it is likely that supernormal stimulation of features associated with need is responsible for the increased provisioning, rather than brood mimicry.

4.1.3 Supernormal stimulation using non-linear vocal phenomena

I found that non-linear phenomena (NLP) were present in the begging vocalisations of both honeyguide species, as well as those of their hosts. Lesser honeyguide nestlings appeared to have higher amplitude modulation (AM) frequencies and perceived roughness than single black-collared barbet nestlings, but not significantly so. These features are both associated with amplitude modulation, suggesting that amplitude modulation is the most likely form of NLP to affect provisioning behaviour in host parents. In a field playback experiment, I therefore tested whether differences between lesser honeyguides and black-collared barbets in the AM frequencies between 11.5 Hz and 28 Hz resulted in different provisioning behaviour by barbet parents. I found no such effect, but these results should be interpreted with caution since amplitude modulation frequencies outside the manipulated range may be important for influencing host provisioning. Additionally, the small sample size meant that the power to detect a difference in provisioning rate was limited. Therefore, it remains inconclusive whether NLPs could be effective avenues for parasitic manipulation.

4.1.4 Differences in provisioning behaviour to playback of lesser honeyguide and black-collared barbet begging calls not replicated

In a previous playback experiment at the same study site, McClean (2020) found that the provisioning rate of adult black-collared barbets was higher when recordings of lesser honeyguide begging calls were played, compared to when recordings of single black-collared barbet nestlings were played. In Chapter 3, I conducted a playback experiment following the same methods and which included these two treatments, but the sound clips used for the playbacks had been manipulated by removing the amplitude envelope between the AM frequencies of 11.5 Hz and 28 Hz and reinserting the amplitude envelope, to control for the effects of manipulations for the other treatments. In my playback experiment, there was no evidence for a difference in barbet provisioning rate between the single barbet and lesser honeyguide treatments. Therefore, the results observed by McClean (2020) were not replicated. I suggest that this could have arisen either because the way I manipulated the “control” recordings removed some feature of the calls that is important for communication of need or identity, or because different environmental conditions between years affected the provisioning decisions of the barbet parents.

4.2 Limitations

The methods and results of this dissertation were limited by several factors, and understanding these limitations is essential to interpret the results. First, all data collected were from the same study site, on four farms north-west of the town of Choma, in the Southern Province of Zambia. Both honeyguide species are widespread and occur across much of sub-Saharan Africa. It would be interesting to know whether similar findings would be made at other locations, or from secondary host species at the same location, since both honeyguide species have different primary host species across their range, as well as many secondary host species. Specifically, host species may differ in their ecological and life-history context, which would affect their provisioning decisions and so the manipulative defences they select for in honeyguides. For example, some other hosts of greater honeyguide, such as red-throated bee-eater (*Merops bulocki*) are colonial, cooperative breeders (Fry, 1974; Fry & Boesman, 2020), others are non-colonial cooperative breeders, such as green woodhoopoe (*Phoeniculus purpureus*) (Ligon & Kirwan, 2020a), whereas others, such as African hoopoe (*Upupa africana*) and common scimitarbill (*Rhinopomastus cyanomelas*) are solitary breeders with only the parents provisioning nestlings (Krištín & Kirwan, 2020; Ligon & Kirwan, 2020b).

I examined two species of honeyguides in a family that includes 16 recognised species, many of which are inconspicuous and hard-to-identify birds of the central African forest zone and have poorly understood natural histories – in fact, eggs or chicks of the majority of honeyguide species have never been seen, and it is only assumed (reasonably) that they are brood-parasitic based on common ancestry (Short & Horne, 2001; Spottiswoode & Koorevaar, 2012; Winkler, Billerman & Lovette, 2020). Future studies will need to assess whether other honeyguide species also mimic their hosts. In other groups of closely-related brood parasites, some members appear to mimic their hosts while other do not. For example, screaming (*Moluthrus rufoaxillaris*) and shiny cowbirds *(M. bonariensis)* both parasitise baywings (*Agelaioides spp.*), but only the screaming cowbird mimics their nestlings (Ursino et al., 2018).

The playback experiment suffered from limited statistical power (71.1%) and from a possibly too conservative experimental manipulation: the experiment also only tested a very specific amplitude modulation envelope that was (between 11.5 and 28 Hz AM frequencies) which was a subset of the possible variation. I chose these envelopes based on the range of AM frequencies in the preliminary analysis. However, since perceived roughness appears to be a feature that varies between host broods and single hosts and honeyguides, and perceived roughness is calculated using AM frequencies above the ones studied, these higher AM frequencies may be important. By only manipulating amplitude frequencies in this range, the roughness was not adequately manipulated in the playback experiment. Therefore, even if amplitude modulation affects host provisioning, it is likely that what may be important lies outside of the range of AM frequencies tested by the experiment. This experiment therefore does not satisfyingly falsify the hypothesis that NLP can be used by brood parasites to manipulate host provisioning.

Moreover, the playback experiment was only conducted in one year (2022), so differences between years in provisioning behaviour in the barbet parents were not accounted for. Depending on the environmental conditions, particularly the availability of food, there may be differences in how the barbets respond to nestling begging calls. Specifically, when food resources are limited, barbet parents would likely respond less to begging call signals and cues, since the maximum rate they are able to provision is constrained (Low, Makan & Castro, 2011).

Finally, we should be open to the possibility that the acoustic metrics I used described the calls imperfectly. I made the decision to limit the number of acoustic metrics of begging call features I used in the correlational analyses in this dissertation, to reduce the risk of false positives due to multiple testing. As a result, the begging call structure is not fully described using these measurements alone. However, I believe I made sensible decisions by carefully choosing the metrics so that one variable describing each major type of acoustic feature (of the numerous metrics provided by the package *warbleR*; Araya-Salas and Smith-Vidaurre, 2017) was included in the analyses.

4.3 Future directions

My results raise several questions to be explored in future research. Additionally, some of the questions I sought to answer in this dissertation require further study since the results were not conclusive.

Particularly, the role of NLP in begging call signalling in general, as well as its use specifically in brood-parasitic manipulation, remains intriguing and requires further investigation. I suggest that NLP remains a plausible hypothetical signal of need in nestling begging calls that is worth examining further, particularly when there are constraints on the pitch and temporal arrangement of elements (e.g. due to begging calls already being at given at their fastest rate or needing to ensure that host parents identify the call as coming from their own nestling). Despite NLP being present in many bird vocalisations, its potential signalling function in birds has received little attention generally, even though it is well understood in mammal vocalisations. Since the results of this study were inconclusive, further examination into the potential use of NLP by honeyguides to manipulate the provisioning rate of the host is required. Further playback experiments with synthetic recordings where specific features are altered by adjusting single parameters of the synthetic models would be able to shed further light on the response of host parents to variation in NLP.

Therefore, the actual mechanism driving the high rate of host provisioning to honeyguides, at least under some conditions, remains a mystery. It may be that none of the hypotheses proposed by this dissertation are actually responsible, and other candidate features could be proposed and tested. For example, neither the structure of individual elements in a syllable, nor the proportion of time spent calling, were examined, and these may provide alternative hypotheses. Other methods of measurement and assessing similarity in features could also be used in future studies, since different measurements or similarity metrics may work better for vocalisations with different salient features (Ranjard et al., 2010). Analysis of modulation spectra and cepstral coefficients are other approaches which could be used to assess the similarity between honeyguide and host recordings (Ranjard et al., 2010). Additionally, similarity analyses could be conducted at different levels of organisation in the calls. For example, methods that compare the structure of individual elements within each syllable and how these elements change through the course of a syllable could be further examined.

There are also likely many unstudied systems in which brood parasites manipulate the behaviour of their host parents through begging calls, or for which the mechanisms are not fully described. Since many brood parasites are scarce and understudied, particularly members of the honeyguide family, there is likely much interesting natural history that remains undiscovered.

We also don't yet fully understand the source of selection on begging call mimicry in honeyguides. The findings that honeyguides do mimic their primary hosts implies that there must be selection imposed by the host parents to sound like their own offspring. This may be either because host parents can discriminate strange calls and reduce provisioning or abandon the nest, or because begging calls that are too different from the hosts' own nestling begging call are not as effective at signalling the amount of food needed. Alternatively, it may be because the host parents have a sensory bias towards a particular feature, and as a result the host parents impose selection on both their own nestlings and the honeyguide nestlings simultaneously. It has been debated whether similarity due to the latter mechanism can be defined as mimicry, since the selection by the receiver on the mimic is not due to the perceived similarity to the model, but because of an inherent bias (De Jager & Anderson, 2019; Grim, 2004). My study cannot distinguish which of the above mechanisms may apply in honeyguides. However, further investigation may provide insights into the selective mechanisms imposed by the host parents on honeyguide nestlings. Specifically studying nest rejection and provisioning behaviour by host parents in response to playbacks of honeyguide begging calls of various degrees of similarity to the nestlings of the host may help understand whether nest rejection or chick discrimination occurs in response to strange begging calls. However, it remains difficult to separate whether differences in provisioning rate to atypical begging calls is due to a sensory bias in the host parent, or to recognition of signals of need by the host parent.

There are many other interesting aspects of host mimicry by honeyguides which could also be explored further. Since both honeyguide species are generalist brood parasites, how are they be able to achieve mimicry? Do they only mimic their primary host, or do they also mimic secondary hosts? If the latter, how is this achieved? For example, examining whether multiple hosts could be mimicked through plastic begging calls that are socially shaped by host parents, or whether general features across a wide range of host species are mimicked. These all require further investigation and could be tested by collecting and comparing begging call recordings from more hosts and from different areas of their ranges using similar comparative methods to this study, along with experiments to test how host-specific begging call mimicry develops.

Since both little bee-eaters and black-collared barbets are resident and are mostly distributed in the Afrotropics, they are probably fairly long-lived and have a short breeding season. They are also facultative cooperative breeders and have a long offspring dependence period (Fry & Boesman, 2021; Short & Horne, 2020). As a result, it would be expected that they are accurate discriminators of brood parasites. This is because they have the opportunity to learn the features of their own nestlings well, they may only be able to raise one brood per season, and the costs associated with each brood are large. The accurate discriminating ability that we expect from the life histories of these hosts may result in the mimicry that we observe in honeyguides. Most studies that have examined brood parasite begging call mimicry in detail have been conducted in north-temperate settings on birds with different life history traits (Jamie & Kilner, 2017). Further work needs to be done to assess how the different life history strategies of tropical birds affect the mimicry and strategies of manipulation by brood parasites.

Comparing closely related brood parasites has been used before to demonstrate mimicry in some brood parasites (e.g. Jamie et al. 2020). However, mimicry is claimed in other systems where other sources of similarity have not been excluded (Jamie & Kilner, 2017). I endorse this phylogenetic approach on these systems that have not excluded other sources of similarity since it demonstrates the process of divergence in related species and convergence on each host species, which provides good evidence of selection by hosts.

4.4 Conclusion

Greater and lesser honeyguides and their hosts provide a good system to conduct comparative studies of begging call mimicry and manipulation, since they are closely related, sympatric, and both parasitise hole-nesting birds, which remove any confounding effects of any visual signals and cues. Additionally, the masterful skills that the community members living at study site use to find nests is invaluable, and this study would not have been possible without them.

This dissertation provides quantitative evidence for primary host begging call mimicry by both greater and lesser honeyguides. Therefore, two more brood parasites join the few others for which quantitative evidence exists to support begging call mimicry (Anderson et al., 2009; Buchart et al., 2003; De Mársico et al., 2012; Gloag & Kacelnik, 2013; Jamie et al., 2020; Langmore et al., 2008; Ranjard et al., 2010; Rivers, 2006). Greater and lesser honeyguides are also examples of generalist brood parasites, whereas most examples of begging call mimicry have been observed in brood parasites specialising on one host species, a circumstance under which specialised mimicry should be easier to evolve.

However, the question of how honeyguides manipulate their host parents remains. I have shown that it is not through elevated call rate, which is the only mechanism previously suggested to increase provisioning by host parents of other brood parasites. It also does not appear to be through brood mimicry of any type, contrary to suggestions of previous authors (Fry 1974; Jubb, 1966; McClean, 2020). Honeyguides must therefore use another, previously undescribed mechanism to increase host provisioning. Since begging calls of honeyguides and their primary hosts are similar in pitch and temporal structure, the presence and quantity of NLP provides an attractive hypothesis for a signal of need in the hosts that honeyguides can exploit. However, the results of the present study are inconclusive as to whether NLP is an important feature for manipulating host parents by honeyguides.

Taken together, the results of this study suggest that mimicry by honeyguides is essential to first trick their host parents into thinking the begging call is coming from one of their own nestling, before honeyguides are able to manipulate their provisioning. Additionally, the presence of NLP as a potential signal of arousal in bird vocalisation needs more attention generally, particularly in the context of begging vocalisations.

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