Vocal mimicry in the spotted bowerbird *Ptilonorhynchus maculatus*

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Declaration

The work contained within this thesis is my own and has not been done in collaboration, except where otherwise stated. The text does not exceed 70,000 words, and no part of this thesis has been submitted to any other university in application for a higher degree.

[redacted]

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Abstract

Vocal mimicry is well documented in songbirds, yet the function of this behaviour is poorly understood. I studied vocal mimicry in a wild population of male spotted bowerbirds *Ptilonorhynchus maculatus* to determine whether there was any support for the proposed functional hypotheses invoked to explain this behaviour.

I collected observational data to determine what species male bowerbirds mimicked and how their mimetic repertoires related to the acoustic environment. Spotted bowerbirds preferentially mimicked the vocalisations of aggressive species, which is consistent with mimicry acting to deter predators or competitors (Batesian mimicry). However, these sounds were also relatively simple in terms of their structure, and may be mimicked purely due to their simplicity and similarity to the species-specific hiss. A survey of mimetic repertoires at three geographically isolated populations revealed a similar pattern in model choice: mimetic repertoires were predominantly composed of aggressive and predatory species but these sounds were also structurally simple.

To test whether mimicry was used in a Batesian context I determined what contexts mimicry was produced in. Consistent with predictions, I found that males did not increase their mimetic rate in the presence of conspecifics but did increase their mimetic rate in response to human activity around the bower.

To determine how mimetic sounds are acquired in this species, I compared the mimetic repertoires of individuals within a population and found that males with bowers closer together mimicked more of the same species than did males with bowers that were further apart. Closer inspection of two of these mimicked sounds revealed that neighbouring males did not produce structurally similar mimicry, which suggests that mimetic sounds are learned directly from the species being mimicked.

Males did not increase their rate of species-specific vocalisation when mimetic rate increased, so these vocalisations are unlikely to serve the same function. Males increased their rate of species-specific hissing when in the presence of conspecifics and this vocalisation is likely to function in intraspecific communication. Males also produced ‘advertisement’ calls when alone at the bower that are likely to attract females to the bower or deter rival males. These vocalisations are a long distance signal that varied in structure in three populations of bowerbird. I discuss potential explanations for geographic variation in the structure of bowerbird vocalisations. Vocalisations may be part of the multi-component sexual signal produced by bowerbirds, but I found no relationship between any aspect of male vocalisation and predicted mating success, so these vocalisations are unlikely to indicate male quality to potential mates or rival males.

In conclusion, it seems most likely that mimicry in this species is used to deter predators or competitors, but I cannot exclude the hypothesis that mimetic sounds are learned as a result of their relative simplicity and salience in the acoustic environment. Furthermore, I have shown that mimetic sounds in this species are most likely acquired directly from the species being mimicked. These findings are a useful step towards understanding the function and evolution of this fascinating behaviour.

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CHAPTER ONE: INTRODUCTION

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I wrote the manuscript with S. D. Healy then R. L. Coe and J. R. Madden commented on drafts. The original manuscript can be found as an appendix at the end of this thesis. I wrote the rest of this chapter in collaboration with S. D. Healy.

Summary

Approximately 20% of songbirds copy the vocalisations of other species or abiotic sounds (Baylis 1982) but the function of this behaviour is poorly understood. Here I review the hypotheses proposed to explain the function of vocal mimicry and conclude that with the exception of brood parasites (Davies 2000), there is little evidence to support any functional explanations. Many of the data concerning song mimicry are consistent with the learning mistakes hypothesis, whereby birds learn simple and common sounds as a by-product of their song learning ability. In this thesis I examine the potential explanations for vocal mimicry in the spotted bowerbird *Ptilonorhynchus maculatus* and attempt to determine how mimicry is acquired in this species.

Introduction

Vocal mimicry, the copying of sounds produced by another species or other parts of the environment, is a poorly understood behaviour. Although mainly documented in songbirds and brood parasites, vocal mimicry has also been reported in parrots and in such diverse non-avian animals as seals, killer whales, dolphins, elephants and orangutans (Pepperberg 1981; Ralls et al. 1985; Foote et al. 2006; Reiss and McCowan 1993; Poole et al. 2005; Wich et al. 2009). Songbirds are the only group that consistently mimic in the wild and approximately 15-20% of songbirds mimic to some extent (Baylis 1982). This ability to learn and reproduce complex songs has been observed for centuries. In one of the first experiments on song learning, Barrington (1773) demonstrated that linnets *Acanthis cannabina* exposed to songs of various birds such as the skylark *Alauda arvensis* learned the songs of those species. This impressive ability of birds to learn complex 'non-normal' sounds has fascinated both scientists and laymen: in 2006 footage of a lyrebird mimicking chainsaws, car alarms and sirens was voted as the British public's favourite David Attenborough moment.

Despite the occurrence of mimicry being noted in a wide range of songbirds the function of this fascinating behaviour is poorly understood. Functional explanations for vocal mimicry are inherently attractive given both the complexity and accuracy of some of the mimicry but several reviews have concluded that there is little compelling evidence to support any of the proposed functions (Kelley et al. 2008; Baylis 1982; Garamszegi et al. 2007). It seems possible that there is more than one such explanation for the existence of vocal mimicry but there are too few appropriate data to confirm this.

A number of possible functional explanations for vocal mimicry have been suggested, falling into two major categories: (1) Interspecific communication, for avoidance of threats and/or competitors; (2) Intraspecific communication, either in a sexual context or for social affiliation.

INTERSPECIFIC COMMUNICATION

The Beau Geste hypothesis

By singing many different types of (species-specific) song, an individual may give a false impression that many individuals inhabit a territory and so deter potential intruders. Krebs (1977) originally proposed this Beau Geste hypothesis to explain the occurrence of large, species-specific song repertoires and Rechten (1978) suggested that it may apply to vocal mimicry, particularly for territorial birds. By mimicking the vocalisations of a wide range of heterospecifics, birds may reduce the chance that competitors for food or other resources enter their territory, especially if these potential intruders are themselves highly territorial and thus pay close attention to vocal signals.

In the 1970's there was anecdotal evidence that some species incorporate heterospecific mimicry into their territorial advertisements, perhaps acting to deter heterospecific competitors (Curio 1978). Not only has there been no subsequent support for the hypothesis in the context of species-specific vocalisations (Yasukawa 1981; Dawson and Jenkins 1983; Haftorn 1995), it is also unclear why heterospecific song would be more effective at deterring potential competitors than conspecific song, unless competitors pay attention to the number of different species heard in an area. If mimicry does function in this way we would expect that territorial males to mimic many different species of bird and to remain hidden from view. This type of mimicry also implies that mimicry needs to be of a high enough quality to fool the receiver so we would expect model sounds be accurately copied.

Batesian acoustic mimicry

Dobkin (1979) suggested that mimics may deter competitors or potential predators by copying the vocalisations of animals that are predatory or agonistic, in a manner akin to that of a palatable species attempting to avoid predation by visually resembling a noxious species (Bates 1862). Competitor species may perceive a threat from an apparent predator or aggressor, avoid entering the territory of the mimic, and thus not compete for resources. The intended audience may also include potential predators that are deterred from attacking the mimic by the threat of encountering another predator (Vernon 1973; Dobkin 1979), or are perhaps confused as to the identity of their proposed prey by the conflicting acoustic signals coming from the mimic (Harcus 1977; Curio 1978). This hypothesis predicts that vocal mimics should learn predator vocalisations and then use those sounds in response to the presence of a predator or a competitor.

Most evidence for mimicry functioning in a Batesian context comes from reports of birds mimicking the vocalisations of predators (Warham 1962; Kaplan 1999; Veerman 1994). One possible example comes from the Australian magpie *Gymnorhina tibicen*, which mimics potential nest predators, the barking owl *Ninox connivens* and the boobook owl *N. novaseelandiae* (Kaplan 1999). However, not only are there no data on the context in which these sounds are used, but, given the diversity of sounds that magpies mimic, it would seem that Batesian mimicry is not the most parsimonious explanation for the mimicry of these two owls. Australian magpies can have a considerable mimetic repertoire, a very small proportion of which is mimicry of predatory species (other mimicry includes rosellas *Platcercus* spp, lapwings *Vanellus* spp and lyrebirds *Menura* spp).

In an experimental test of the Batesian mimicry hypothesis, burrowing owl *Athene cunicularia* hisses (claimed to be mimicry of rattlesnake rattles) were played to ground squirrels, eliciting more avoidance behaviour from ground squirrels sympatric with rattlesnakes than from rattlesnake-naïve ground squirrels (Rowe et al. 1986). Playback of rattlesnake noise elicited a stronger response from the ground squirrels than did the owl hiss, but it is not clear whether the owls naturally use this hiss in a defensive response to rattlesnakes, a potential nest predator, or whether it functions to deter ground squirrels from competing for nest burrows. Importantly, this is unlikely to be vocal mimicry as there is no evidence that these hisses are learned, rather, they appear to be a modified juvenile begging call and are the result of call convergence (Owings et al. 2002).

Competition

One of the most common examples of mimicry involves species (usually closely related) with similar ecological niches including heterospecific sounds in their own vocalisations, seemingly so as to reduce aggression over territory boundaries (Baptista and Catchpole 1989). For example, great tits *Parus major* may include blue tit *P. caeruleus* songs (which sound significantly different) in their own vocalisations (Gorissen et al. 2006). There are at least two possible explanations for this kind of mimicry: firstly, due to competition for resources, mimicry of competitor species may be used as an aggressive signal towards that species. Vocal signals play an important role in interspecific territoriality (e.g. Martin and Martin 2001; Gil 1997) and phrasing a threat in the receiver's own language may be the most effective method of territory defence. Alternatively, it could be that great tits, because they interact so frequently with blue tits, mistakenly learn blue tit song. Discrimination between these two would be possible if the use of heterospecific mimicry leads to a reduction in aggressive interactions with those heterospecifics. Other instances where mimicry is produced by a small number of birds seems best explained by copying of an inappropriate tutor as occurs when individuals are isolated or when allopatric species occasionally overlap (Helb et al. 1985).

Attracting a third species

Mimics might benefit by using mimicry to induce mobbing of their own predators or competitors by heterospecifics. Alternatively, mimicry of alarm calls may attract a second predator, possibly coming in search of injured prey, giving the caller a chance to escape during the ensuing contest with the first predator (Hogstedt 1983; Curio 1978). While this might explain the use by phainopeplas *Phainopepla nitens* of mimicry of heterospecific alarm calls when distressed (e.g. when captured in mist nets) as it can elicit mobbing by heterospecifics, it does not fit with the stronger mobbing response evoked by playback of the phainopepla's own alarm calls (Chu 2001a, b). At the very least, this seems an inefficient use of mimicry. Eastern towhees (*Pipilo erthrophthalmus*) will also substitute their own alarm calls with mimicry of heterospecific alarm calls when disturbed. It is not yet clear what benefit is gained by doing this as behavioural responses of heterospecifics and conspecifics were not investigated (Greenlaw et al. 1998).

Sri-Lankan magpies *Urocissa ornata* mimic the vocalisations two predators when mobbing, which may be an anti-predator response (Ratnayake et al. 2010). However, it is not yet clear that these vocalisations either attract assistance from heterospecifics or have any effect on the heterospecific being mobbed. Greater racket-tailed drongos *Dircurus paradiseus* produce heterospecific mobbing calls when mobbing but, again, there is no evidence that these calls elicit mobbing behaviour in other species (Goodale and Kotagama 2006a). Drongos also produce mimicry of heterospecific alarm calls in alarm situations but this is done only as they increase the number of their own alarm notes and not all of the calls produced are alarm calls. Here, the rate of species-specific alarm calling is assumed to be a proxy for a dangerous context but the correlation between species-specific alarm calling and alarm mimicry does not provide direct evidence that mimicry is produced when drongos are alarmed.

Increasing foraging efficiency

Mimicry may also be used to increase foraging efficiency by manipulating the behaviour of others. Greater-racket tailed drongos are usually found in mixed species flocks as these flocks allow them to forage more efficiently, both by catching insects disturbed by flock mates and by kleptoparasitism (King and Rappole 2001). It has been proposed that when outside flocks they mimic non-alarm sounds to attract other birds to form flocks (Goodale and Kotagama 2006b). Playbacks of drongo non-alarm mimicry were more likely to attract other birds than were playbacks without mimicry and, intriguingly, the species attracted were not usually those species being mimicked. This is the first indirect evidence that mimicry may serve more than one function within a species although more compelling examples that the appropriate mimicry is produced in the appropriate context are required.

Facilitating brood parasitism

Brood parasites face discrimination by their hosts and are commonly rejected at the egg stage, driving the evolution of visually mimetic eggs (Davies 2000). Hosts may also discriminate against brood parasite nestlings, perhaps noting the differences in begging calls that they give. To counter this, brood parasite nestlings may have been selected to produce begging calls very like those of their host young. This may be mimicry by direct copying, especially if the parasite is raised alongside host young, so gaining an opportunity for learning the host chicks' begging calls (Redondo and Dereyna 1988). However, as this similarity in vocalisation has also been described for cuckoo species that eject the host's young and are raised alone, it is likely that this is not vocal mimicry but call convergence (McLean and Waas 1987; Madden and Davies 2006).

Vocal mimicry has been demonstrated in the brood parasitic finches *Vidua* spp, which mimic the songs of their host species, the estrildid finches (subfamily Estrildinae). Most of these brood parasites are host specific, whereby one species of *Vidua* parasitizes one species of estrildid finch (Payne 1998; Payne et al. 2005). Male brood parasites learn the song of their host species and later in life they use the song of their host species to attract a mate, who later lays her eggs in the nest of the original foster species (Payne et al. 2000). Unlike brood parasites whose calls have evolved through call convergence, *Vidua* finches demonstrate host plasticity: when the village indigobird *V. chalybeata* was experimentally foster-reared by Bengalese finches *Lonchura striata* they developed songs similar to their new foster parents, despite being able to hear and see red-billed firefinches *Lagonosticta senegala*, their usual host (Payne et al. 1998). Irrespective of host species, indigobird males did not copy songs directly from their host parents (unless isolated with them after fledging) but of other adults of the foster species or other indigobirds mimicking the same foster species. Learning host songs may occur in two stages: early life when the general features of host song are learned from parents, and a later developmental period when songs are learned from non-parents. The occurrence of mimicry in passerine brood parasitic species is one of the few established functions of vocal mimicry but as it is only relevant to this subset of species, we will not consider it further here.

INTRASPECIFIC COMMUNICATION

Sexual selection

The occurrence of mimicry might be explained by sexual selection if mimetic vocalisations provide an honest indicator of male quality (Zahavi 1975), with only the best males being able to learn and give accurate renditions of mimicry (Loffredo and Borgia 1986; Nowicki et al. 2002). Alternatively, females might demonstrate a preference for novelty, which could be achieved by a male by incorporating heterospecific song into his display (ten Cate and Bateson 1988). However, if females were only interested in repertoire size we would expect high levels of improvisation or invention (Kroodsma et al. 1997).

The occurrence of mimetic sounds in the courtship displays of satin bowerbird *Ptilonorhynchus violaceus* males is consistent with mimicry playing a role in mate choice: males may include mimicry of up to five sympatric bird species alongside species-specific vocalisations in their courtship display. While older males tended to produce longer and higher quality bouts (of mimicry of laughing kookaburra *Dacelo novaeguineae* calls, spectrograms assessed by eye) than did younger males, in only one of two years in which mimicry was quantified did mimicry duration and quality result in higher mating success (Loffredo and Borgia 1986). A more recent study showed that male satin bowerbirds' mimetic accuracy of both kookaburra and Lewin's honeyeater (*Meliphaga lewinii*) calls was positively correlated with mating success and accuracy was correlated positively with repertoire size (Coleman et al. 2007). However, these satin bowerbirds mimicked only five species, two of which featured only rarely in the vocal displays, suggesting that much potential for expanding repertoire was not being used. The possibility that satin bowerbird females prefer sounds that are physically difficult for males to produce (rather than a large repertoire) has not been investigated. For a signal to be honest it must reflect performance limits (Podos 1996; Allan and Suthers 1994), for example female canaries *Serinus canaria* are sensitive to particular phrases in male courtship song that are physically complex to produce (Vallet et al. 1998; Vallet and Kreutzer 1995).

There is some evidence that quality of mimicry increases with male age in the satin bowerbird (Loffredo and Borgia 1986), which may be linked to female preference for vocalisations that are complex and difficult to mimic. However, male satin bowerbirds mimic calls and not songs and the calls they mimic do not appear to be very complex. Mimetic ability provides a loose indicator of male age in superb lyrebirds *Menura novahollandiae*, as subadults produce less accurate mimicry and have smaller repertoires than adults (Zann & Dunstan 2008). Although these data are consistent with mimicry playing a role in mate choice, alternative hypotheses cannot be excluded without explicitly testing the relationship between mating success and variation in mimetic quality and/or repertoire size.

In the only other species for which there has been an investigation into the relationship between mimicry and mating success, male black-browed reed warblers *Acrocephalus bistrigiceps* sing long, complex songs but do not achieve higher mating success (as measured by pairing date) when the mimetic component of their repertoire is higher (Dowsett-Lemaire 1979; Hamao and Eda-Fujiwara 2004).

Social affiliation

The ability to match vocalisations of conspecifics for social cohesion has been reported in several species of birds and is likely to be prevalent in the taxa that learn their vocalisations (Cortopassi and Bradbury 2006; Vehrencamp et al. 2003; Hile et al. 2000). Robinson (1991) suggested that lyrebirds *Menura* spp. might use vocal mimicry in this kind of way, too, for maintaining contact in the dense rainforest in which they live. However, the value of using mimicry rather than species-specific calls to maintain contact is unclear. It may be that certain types of song transmit especially well in certain habitats and that it is more cost effective to copy these from the environment than it is to establish them as part of a species-specific repertoire. Satin bowerbirds produce calls that have been shown to be locally adapted to enhance transmission (Nicholls and Goldizen 2006). Albert's lyrebirds (*Menura* *alberti*) mimic these local satin bowerbirds calls possibly to produce effectively transmitted sounds (Putland et al. 2006). However, this fails to explain why the lyrebirds mimic many more environmental sounds than just the most efficient call type. Importantly, models do not respond to lyrebird mimicry and there are, as yet, no data on the response by lyrebirds to mimicry produced by conspecifics.

Learning Mistakes Hypothesis

In 1984, Hindmarsh suggested that mimicry in the European starling *Sturnus vulgaris* may be a result of mistakes made during song learning and therefore the mimicry serves no function. If mimicry is indeed a collection of sounds mistakenly picked up during song learning, rather than a result of specific learning, we would expect one or more of the following: (1) mimetic repertoires would contain notes that are similar to the species-specific repertoire; (2) simple sounds would be mimicked more often than expected by chance; (3) mimetic repertoires would contain sounds that are commonly heard or loud; (4) mimicry is not always used in the appropriate context.

In one of the few studies to test the predictions of more than one hypothesis, mimicry in robin chats *Cossypha* spp. is consistent with several predictions that come from the learning mistakes hypothesis: robin chats are more likely to mimic simple songs and do not mimic significantly more predators or competitors (Ferguson et al. 2002). There was no correlation between model prevalence in the acoustic environment and presence or absence in the mimetic repertoire: many species that were commonly heard at study sites were never mimicked and several mimicked models were never heard at that site. However, the mimetic repertoire of the black-browed reed warbler (see above) does seem to be a reflection of the sounds of the common birds in their environment rather than of any specific group of species (Hamao & Eda-Fujiwara, 2004), as is that of the marsh warbler *Acrocephalus palustris* (Dowsett-Lemaire 1979).

There is at least one prediction that follows from the learning mistakes hypothesis that could readily be tested: we would expect to hear mimicry often being used in inappropriate contexts. However, due to our poor understanding of what sounds are learned, how and in what context, it is difficult to test the potential predictions of this hypothesis. For example, while it seems plausible that sounds that are similar to species-specific vocalisations are more likely to be learned in error than are dissimilar sounds, there is, as yet, little relevant evidence. The plausibility of such an idea is enhanced by findings such as the learning by song sparrows (*Melospiza melodia*) of swamp sparrow (*M. georgiana*) songs if the swamp sparrow syntax is edited to have a similar syntax to song sparrow conspecific songs (Marler and Peters 1988).

If mimicry is a result of making mistakes during song acquisition, then the acquisition of the sounds should be confined to the stages at which normal song learning occurs (Hindmarsh 1986a). In closed-ended learners we would expect the mimetic repertoire to be fixed at the same time as the species-specific song is fixed. Open-ended song learners that modify their species-specific song repertoires throughout life would have greater opportunities to learn new sounds and may therefore learn more heterospecific songs by mistake.

The mimicry of alarm calls and of predatory species might also be explained through mistaken learning. This is because learning about any particular individual, location, object or event is always affected by the motivational state of the learner, which in itself is affected by stress. Although high acute stress (which itself may be good or bad) may make it difficult to recollect remembered information at the time, it is often correlated with good acquisition of information and long-term retention of that information (Rowe 2002). Hearing predators or alarm calls of other prey species is likely to increase stress levels acutely and may lead to enhanced uptake of lots of information pertinent to that instance. Not only would this lead to learning the specific sound, it may also lead to learning the context in which that sound was heard (Greenlaw et al. 1998). Such one-trial learning of complex information is the hallmark of learning to avoid unpalatable prey, imprinting, snapshot memory and, indeed, all episodic memory. Later production of a sound learned in a specific context may be expected to occur when the context is reproduced or when the animal is stressed. This would explain all of the apparent intentional insertion of mimicked alarm calls into alarm calling and mobbing in the appropriate context. As the neural structures underlying call production are thought to be different from those operating in song learning (Simpson and Vicario 1990), it may also be the case that mimicry of song or complex sounds differs significantly in other ways from that of alarm calls.

The relationship between mimicry and species-specific vocalisations

If mimicry is learned in error alongside the species-specific repertoire we would expect that birds with larger species-specific repertoires would be more susceptible to acquiring heterospecific vocalisations. Hindmarsh (1986b) concluded that mimicry was present in passerine species that had complex songs in terms of song length, variability and repertoire size. Another study that controlled for phylogenetic relationships and research effort concluded that mimicry was more prevalent in species that had long songs, short intervals between songs and large syllable repertoires (Garamszegi et al. 2007). These findings suggest that species-specific song complexity is a good predictor of the occurrence of mimicry in a species.

It is poorly understood how mimicry relates to the species-specific repertoire within a species as very few studies specify whether mimetic vocalisations are interspersed with species-specific vocalisations or whether they are produced in isolation from other sounds. Mimicry may act to enhance a species-specific signal (for example by increasing repertoire size during sexual display) in which case we would expect mimicry and species-specific vocalisations to occur together. If mimicry serves a unique function in the vocal repertoire, for example by trying to deceive a predator as the identity of their prey, then species-specific sounds should not be produced alongside mimicry. Comparisons between the structures of mimicked sounds and species-specific sounds can also be used to infer functions of mimicry. One of the predictions from the learning mistakes hypothesis is that sounds that are similar to species- specific vocalisations are likely to be learned in error, yet there are no data to support or refute this.

How is mimicry learned?

Considering how well song learning is understood (Catchpole and Slater 2008) it is perhaps surprising how little we understand about how mimetic sounds are acquired. Understanding the acquisition of mimicry could help to address associated questions such as how/if models are chosen. For example, reports of sedentary starlings mimicking species that are found many miles away seem best explained by the mimicry passing from one starling to another (Hausberger et al. 1991). This process may also maintain mimetic calls across many generations, but not always: starlings introduced to New Zealand in the 19th century are proficient mimics but their mimetic repertoire does not contain calls from any non-introduced European birds (Hausberger et al. 1991). Once a mimicked sound is part of a bird's repertoire it may then be learned by a conspecific as part of the overall species-specific repertoire and, as such, would no longer be mimicry. Marsh warblers cease singing before their young hatch and repertoires are learnt entirely from heterospecifics, copied from species at both their European breeding grounds and Africa, where they over-winter (Dowsett-Lemaire 1979). Local mimetic 'dialects' of Albert's lyrebirds indicates vocalisations are learned directly from models, although the stereotyped sequence of different models produced during a mimetic bout suggests this component of mimicry is transmitted between conspecifics.

As yet we do not know whether any selectivity of model is accompanied by auditory or physiological constraints on models that are mimicked. Bill and vocal tract morphology are likely to limit the rate of syllable repetition and hence the type of models that a species is able to mimic (Podos 2001). Songbirds use both sides of the syrinx independently during song production and mockingbirds *Mimus polyglottus* that produce more accurate mimicry use an identical motor pattern to their model species (Zollinger and Suthers 2004). When mimicking songs with notes outside their frequency range, mockingbirds either substitute a note within their frequency range, or omit the note. When notes are omitted other notes in the sequence are lengthened, so that the song is identical in duration to the model song, as if in recognition that song duration is important. When mimicking songs with high syllable repetition rates such as the canary *Serinus canaria*, mockingbirds cluster notes into discrete groups due to pauses for inspiration but, again, maintain the overall song length. In mockingbirds, at least, there may be physiological constraints on the accuracy of mimetic songs. By investigating these questions in other mimics, we would be able to examine whether species with smaller mimetic repertoires are physiologically constrained in the models that they mimic, or whether they have other constraints acting upon them.

VOCAL MIMICRY IN BOWERBIRDS

The bowerbird family (Ptilonorhynchidae) is endemic to Australia and Papua New Guinea (Frith and Frith 2004). They are most famous for their impressive bower building behaviour where polygynous males construct, maintain and decorate complex structures that are the target of female choice. It is perhaps because of this unusual behaviour that the occurrence of mimicry in bowerbirds has been largely overlooked until recently. Mimicry has been reported in 17 of the 20 species in the Ptilonorhynchidae family. The three species of monogamus catbird (*Ailuroedus* spp.) where no mimicry has been reported also do not build bowers and are thought to be ancestral to the other bowerbirds (Kusmierski et al. 1997). Bowerbirds mimic the vocalisations of other avian species as well as human speech, fluttering wings, dripping water and a whip crack (Frith and Frith 2004).

Mimicry during courtship has been reported in many bowerbird species apart from the grey bowerbirds (previously Chlamydera genus, now Ptilonorhynchidae; Christidis and Boles 2008). Most of the data on mimicry in bowerbirds comes from work on the satin bowerbird *Ptilonorhynhcus violaceus,* where males include mimicry into their courtship displays. Older males produced more accurate mimicry and mimicked for longer than younger males, and these courtship vocalisations were associated with higher mating success (Loffredo and Borgia 1986). Males with larger mimetic repertoires also had higher mating success than males with smaller repertoires (Coleman et al. 2004). These findings suggest that females may use mimicry to assess male quality but it is not known whether satin bowerbirds also mimic in other contexts. For example, tooth-billed bowerbirds *Scenopoeetes dentirostris* produce mimicry during courtship, opportunistically when flocks pass by and in duet with the species being mimicked (Frith and Frith 2004). In contrast to other bowerbirds, the grey bowerbirds do not mimic during courtship. Indeed, several observations of female grey bowerbirds producing mimicry when disturbed at the nest have been interpreted as predator defence (Warham 1962; Frith and McGuire 1996).

Spotted bowerbirds *Ptilonorhynchus maculatus*

Male spotted bowerbirds *Ptilonorhynchus maculatus* include the vocalisations of predators in their mimicry (Coe 2005). This mimicry may be deceptive as Chisholm (1932) noted that mimicry was produced at a similar amplitude to the model vocalisation, unlike in other species of mimics where mimicry is produced in quiet subsong. Mimetic sounds may also be accurate enough to deceive heterospecifics: spotted bowerbird mimicry of a kite caused a hen and her chicks to seek cover (Warham 1962). However, there are no reports of mimicry occurring during natural predation events or of predators being deterred by mimicry.

It is unclear how mimicry functions in the spotted bowerbird and how these sounds are acquired. Spotted bowerbirds have a relatively simple species-specific repertoire, which consists predominantly of harsh broadband hisses and ‘advertisement’ calls. Other sounds in the species-specific vocal repertoire include cat-like yowls, ‘squawks’ and mechanical sounds (Frith and Frith 2004).

Of the proposed hypotheses explaining the occurrence of vocal mimicry, it seems most likely that mimicry in spotted bowerbirds is used in a Batesian context to deter predators or competitors (Coe 2005). This leads to several testable predictions: (1) mimetic repertoires should be predominantly composed of predatory or aggressive species; (2) this type of model should be mimicked throughout the species range; (3) mimicry should be produced in the presence of the intended receiver, in this case potential predators or competitors and this mimicry should be of predatory or aggressive species. I recorded the vocalisations of a population of spotted bowerbirds to determine what species were mimicked and whether they were produced by species that were predatory or aggressive. Further recordings of bowerbirds were made at two other geographically isolated sites to establish whether the types of models mimicked were repeatable over large distances. I also measured the rate of mimicry in different social contexts to determine whether mimetic rate increased when in the presence of potential predators or competitors. These data were then used to determine whether they met the predictions of the Batesian mimicry hypothesis, and whether they were also consistent with any of the alternative hypotheses, particularly the sexual selection hypothesis. The acquisition of mimicry is poorly understood, and I investigated geographic variation in the mimetic repertoires to establish how the repertoires of males within a population relate to each other. I then looked in detail at the structure of mimetic sounds to establish whether these sounds are learned from other bowerbirds or directly from the model species.

CHAPTER TWO: The content of mimetic repertoires

I collected and analysed the data. James Nicholls independently corroborated sounds suspected to be mimicry and categorised species. I produced the first draft of the manuscript, which was then completed in collaboration with S. D. Healy.

Summary

Although vocal mimicry in songbirds is well documented, little is known about the function of such mimicry. One proposed functional explanation is Batesian acoustic mimicry, where a mimic produces vocalisations of predatory or aggressive species to deter potential predators or competitors from entering an area. I determined the contents of mimetic repertoires of individuals in a population of male spotted bowerbirds *Ptilonorhynchus maculatus*. I identified what model species were being mimicked and whether these species were predatory, aggressive or competitor species. Male mimetic repertoires contained an overabundance of vocalisations produced by species that were generally aggressive. These sounds tended to be structurally simple and may be mimicked due to their relative simplicity. However, other simple sounds that were common in the sound environment were not mimicked and complex sounds were also present in mimetic repertoires. These findings suggest that mimicry may function to deter heterospecifics or conspecifics.

Introduction

There are multiple explanations for the existence of mimicry of heterospecific vocalisations (Kelley et al. 2008; Baylis 1982). Sexual selection and social affiliation are the most commonly invoked causes of this behaviour in avian and non-avian mimics respectively (Coleman et al. 2007; Zann and Dunstan 2008; Poole et al. 2005; Ralls et al. 1985). An intriguing alternative possibility in many songbirds is that mimicry is used to deter potential predators (acoustic Batesian mimicry; Dobkin 1979). The Batesian mimicry hypothesis posits that mimicry of the vocalisations of predatory or aggressive species may be produced to deter predators or competitors. For example, Australian magpies *Gymnorhina tibicen* mimic two species of potential nest predators (Kaplan 1999). However, magpies also mimic non-predatory species so Batesian mimicry is perhaps not the most parsimonious explanation for mimicry in this species. Indeed, most reports of possible use of mimicry in a Batesian context involve anecdotal observations of an individual mimicking the vocalisations of a predator (Chisholm 1932; Frith and Frith 1990).

There are several ways to examine whether Batesian mimicry is a good explanation for mimicry. The first is to present a mimic with a potential predator and determine whether mimicry of predatory species is produced in response. The second is to play recordings of mimicry to possible intended receivers of mimicry; for example if mimicry serves a Batesian context to deter other bowerbirds we would expect recordings of mimicry to elicit anti-predator behaviour from the focal bird. The third is to examine in detail the entire repertoire of a mimic to determine which model species are copied and whether these are primarily potential predators. However, predatory species often produce loud simple calls and mimicry of those calls may be due, in fact, to that simplicity or loudness i.e. it is the structural features of the predator's vocalisations that lead to those sounds being preferentially mimicked and not because of the meaning contained within the sounds. Classically, the term Batesian vocal mimicry is used to describe vocal mimicry of predators used to deter predators, but may also be directed at other heterospecifics and/or conspecifics. A plausible extension of this hypothesis is that mimicry of aggressive or competitor species could be used in a similar way to deter competitor heterospecifics and/or conspecifics (Rechten 1978; Gorissen et al. 2006). By examining in detail the sounds produced by both model and mimic it may be possible to determine whether predatory, aggressive or competitor species are primarily mimicked and whether that mimicry is better explained by simplicity or some other structural feature.

The grey bowerbirds (previously Chlamydera) have all been reported to produce mimicry of predatory species (Frith and Frith 2004). I attempted to record the entire mimetic repertoire of a population of male spotted bowerbirds *Ptilonorhynchus maculatus* at Taunton National Park in central Queensland, Australia, during two sequential breeding seasons. As these birds typically include predatory species in their mimetic repertoire it is plausible that they do so in order to deter predators, competitors or conspecifics (Coe 2005). With regard to repertoire content the clearest predictions from the Batesian mimicry hypothesis lead to the prediction that the mimetic repertoire of these birds would be composed overwhelmingly of predatory species. I also compared sounds that were present in the mimetic repertoire with sounds that were common in the acoustic environment to determine whether sounds with particular structural properties were preferentially mimicked.

Methods

I recorded the vocalisations of 19 male bower-owning spotted bowerbirds in Taunton National Park (23.3ºS, 149.1ºE), central Queensland, Australia, in July to November 2007 and 2008. Individuals were identified by a unique series of colour bands on both legs. Males were recorded vocalising at their bowers using a Sennheiser ME66/K6 microphone onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. All recordings were carried out by an observer sitting approximately 10-15m from the bower and took place between 5:00am and 2:00pm. Recording sessions lasted between three and seven hours and the average time spent recording at each bower was 16 ± 0.95 hours (mean ± SE) per bower in 2007 and 17.13 ± 2 hours in 2008.

All recordings were converted into spectrograms using Raven Pro v1.3 (Charif et al. 2004) using a Hann window and a 512 pt fast Fourier transform. Species-specific vocalisations ('hissing') were isolated and a representative recording of a hiss was chosen for comparative analysis with mimetic sounds. Mimicry was identified by listening to recordings and by visually inspecting spectrograms. Models were recorded opportunistically around bowers. In the absence of a recording of a model species I used recordings from the Simpson & Day (1999) CD-ROM of bird sounds. To determine which mimicry was that of a putative model I compared model sounds with those of the mimic first by ear and then by comparing spectrograms (Figure 1). An ornithologist (J. A. Nicholls) with over ten years experience of Australian birds and who was familiar with Taunton National Park later corroborated all sounds identified as mimicry.

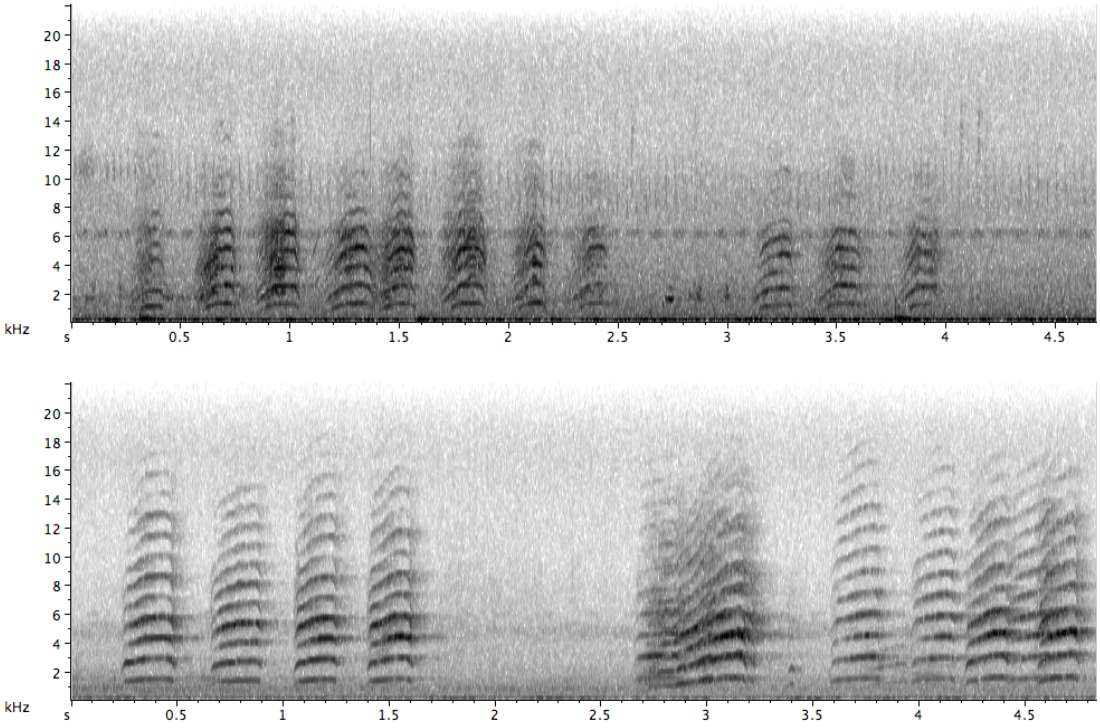


Figure 1. Top: spectrogram of suspected mimicry of a yellow-throated miner (*Manorina flavigula*) model; bottom: spectrogram of a yellow-throated miner vocalisation. Time in seconds is represented on the x-axis, frequency in kHz on the y-axis and the amplitude is represented by the shade of grey/black.

I constructed repertoire profiles for all male bower owners in 2007 and 2008. These data were also combined with data collected by Coe (2005), detailing the repertoire size and composition of four males that have owned bowers since 2002. To determine the nature of mimicked sounds I investigated what models bower owners mimicked from the suite of sounds available in their acoustic environment. I compiled a list of species present at Taunton using the Atlas of Australian Birds (using www.birdata.com.au, an online resource that lists all birds observed within a defined area) and checked that the listing matched up with species seen or heard during my observations. I reduced the list to the 40 species most commonly heard in 2007 and 2008 by identifying and noting down birds that were heard or seen during the course of observations and ranking them in order of prevalence. Of these, 13 species were mimicked by bowerbirds and 27 were not. All 40 species were then classified as predatory if they predated upon bowerbirds, aggressive if they behaved aggressively towards bowerbirds (for example by displacing them from a perch) and as food competitors based on their diet. Spotted bowerbirds are primarily frugivores so any species whose main source of food was fruit and berries was classified as a competitor. Birds were classified using personal observations and using size, habitat and diet information from Simpson and Day (1999), and species could be assigned to more than one group. These 40 species were also re-classified according to whether they were generally predatory or aggressive to non-bowerbird species (for example, the whistling kite *Haliastur sphenurus* is not a predator of bowerbirds but will predate upon smaller birds). J. A. Nicholls also classified all 40 species into these five groups without prior knowledge of whether they were mimicked or not, and a consensus was reached as to the categorisation of all 40 species. I also classified the 40 species into two groups of 20 species categorised at ‘common’ or ‘rare’, based on the prevalence data collected at bowers. Binomial logistic regression was then used to test whether bowerbirds were preferentially mimicking a particular type of species.

To address whether sounds with certain structural properties were preferentially mimicked, I measured the maximum frequency, minimum frequency, frequency range, peak frequency and duration of the 40 models from recordings taken at Taunton and from professional recordings for species where no field recordings were obtained (Simpson and Day 1999). Using categories described by Hindmarsh (1984; Figure 2) sounds were also scored for complexity in frequency structure and frequency modulation. These terms were then entered into a binomial logistic regression.

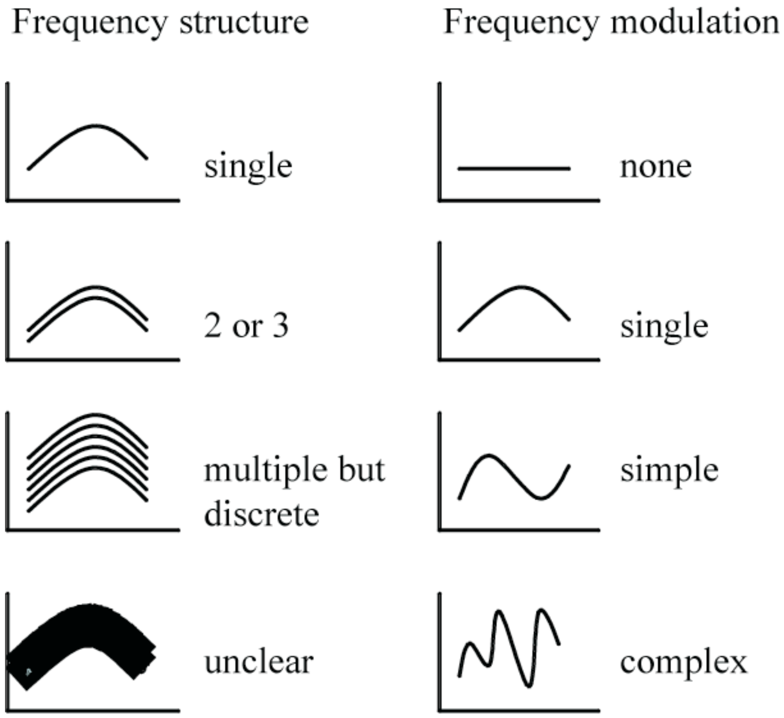


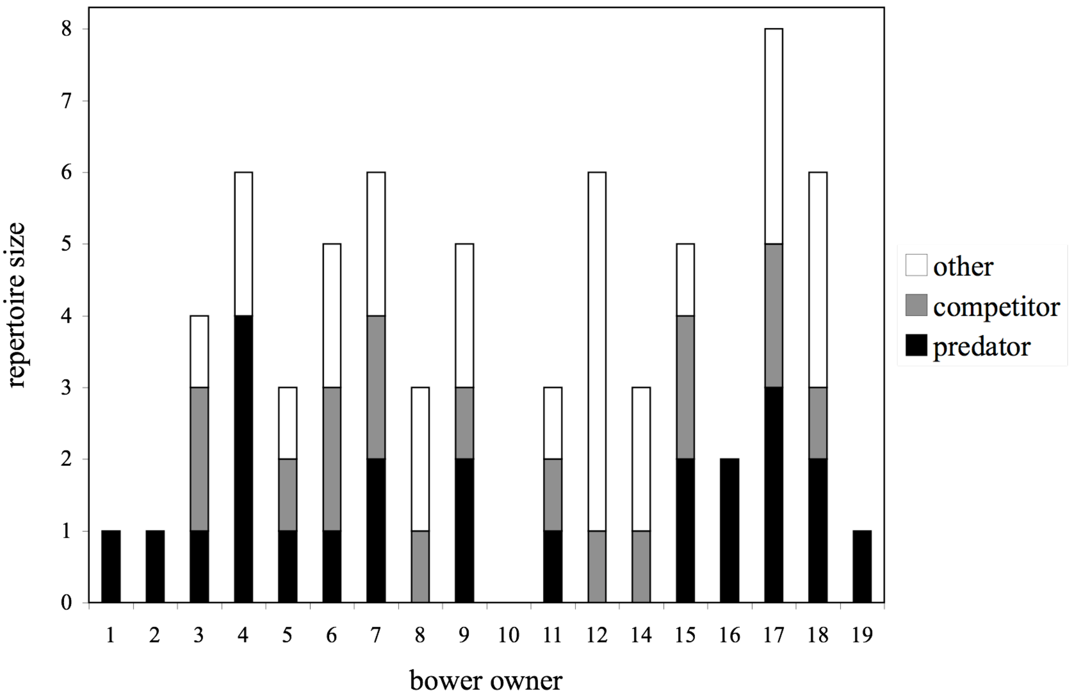
Figure 2. Categories used to classify the complexity of sounds using frequency structure (left) and frequency modulation (right). The x-axis represents time and the y-axis represents frequency.

The data were manipulated and analysed using Excel, Jmp and SPSS (v. 13). All data were tested for normality in SPSS using the ratio skew: SE skew < 3 (Sokal and Rohlf 1994).

Results

Individuals varied in the size and composition of their mimetic repertoires in both 2007 and 2008 (Figure 3a & b). The range of models mimicked was zero to eight, and the most commonly mimicked species was the brown falcon *Falco berigora*. Although individual males tended to mimic a different number of models each year, the repertoires of males within the population did not consistently increase or decrease in size between years (paired t-test f = -1.092, $p = 0.29$). The repertoire sizes of the four males that had been bower owners since 2002 also did not change in a consistent manner (GLM: $F_{(3,15)} = 1.01$, $p = 0.43$).

(a)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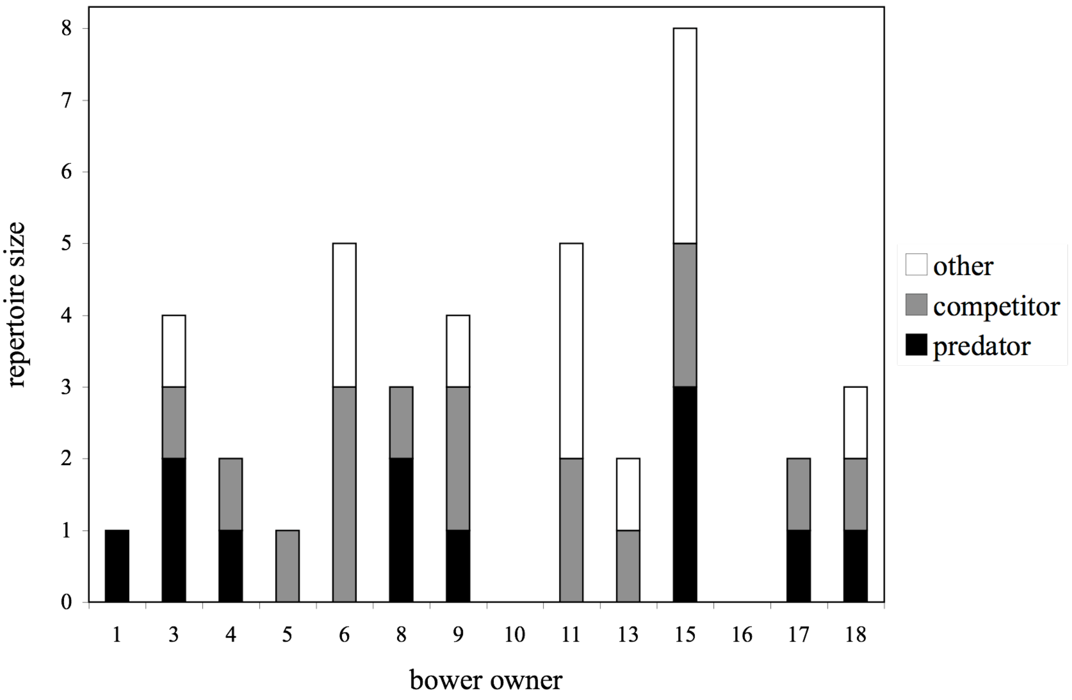
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Figure 3(a) Size and composition of mimetic repertoires of bower owners in 2007. Each bar represents one bower owner; (b) Size and composition of mimetic repertoires of bower owners in 2008.

Males mimicked species that were generally aggressive (Wald $\chi^2 = 9.64$, $p = 0.002$). Males mimicked sounds that had multiple or unclear frequencies and sounds that had a single frequency were under-represented in the mimetic repertoire (Wald $\chi^2 = 6.48$, $p = 0.01$). Mimicked sounds also had relatively high minimum frequency (Wald $\chi^2 = 5.72$, $p = 0.02$) and relatively low peak frequency (Wald $\chi^2 = 4.25$, $p = 0.04$) when compared to non-mimicked sounds. Males mimicked sounds that had the same frequency structure as the species-specific hiss (Wald $\chi^2 = 7.03$, $p = 0.008$). There were no similarities between the hiss and mimicked sounds in terms of frequency modulation (Wald $\chi^2 = 1.90$, $p = 0.17$).

Discussion

Spotted bowerbirds preferentially mimicked species that were generally aggressive species but they did not preferentially mimic predatory or competitor species. The species mimicked were not more common in the acoustic environment than were species that were not mimicked. Mimicked sounds also shared several structural properties with the species-specific hiss when compared to non-mimicked sounds.

The majority of the male spotted bowerbird vocal repertoire is comprised of aggressive models. This is consistent with the prediction from the Batesian mimicry hypothesis that mimicry in this species is acting to deter predators, competitors or conspecifics. Given that models that are predatory or aggressive to bowerbirds were not preferentially mimicked, it seems that the models mimicked would be most likely to deter heterospecifics rather than conspecifics. However, to confirm that this is the case we would need to demonstrate experimentally that mimicry is used in this way. I would also be cautious in interpreting mimicry in this species as due to Batesian mimicry because many of the mimicked sounds were structurally similar to the species-specific hiss. This may mean that the bowerbirds learn these calls much more readily than they do sounds that do not share these features. It would be useful to examine the similarity between structural features of mimicry and models in other populations of spotted bowerbirds and, indeed, in other species to determine whether this is the case. To do this a complete set of recordings of the mimetic repertoire and of the acoustic environment are required.

The specific content of a mimic's repertoire (i.e. predator, competitor) does not obviously help to address the predictions of the two more common hypotheses proposed to explain the occurrence of vocal mimicry: sexual selection and social affiliation (Loffredo and Borgia 1986; Robinson 1991). If the repertoire acts chiefly to advertise to conspecifics in a sexual selection context I would not expect an overabundance of predatory species i.e. there are no specific predictions as to which species in the environment should be mimicked (e.g. as a useful indicator of quality). However, it could be argued that the mimicked calls should be more complex than non-mimicked calls, which they are not (Zann and Dunstan 2008; Coleman et al. 2007). The predictions from the social affiliation hypothesis are much less clear with regard to content of the repertoire. Support for those predictions would require investigation into the context in which mimicry is produced.

Most work to date on investigating the function of vocal mimicry has concerned itself with what mimicry is produced in one particular context (Coleman et al. 2007; Ratnayake et al. 2010; Goodale and Kotagama 2006a). I would suggest that useful insight into the function of vocal mimicry can be gained by methods such as I describe here i.e. recording and examining the structure of a complete vocal repertoire. Such analyses underpin much of the research into the function of non-mimetic song (e.g. Nowicki et al. 2002; Beecher et al. 2000; Franco and Slabbekoorn 2009). Furthermore, such data can provide some understanding of the learning involved, about which little is currently known (Kelley and Healy 2010; Putland et al. 2006).

CHAPTER THREE: THE CONTEXT OF VOCAL MIMICRY

I collected and analysed the data and produced the first draft of the manuscript, which was then completed in collaboration with S. D. Healy.

Summary

Although vocal mimicry in songbirds is well documented the function of such impressive copying is poorly understood. Observing a mimic in a range of naturally occurring contexts and identifying those in which mimicry occurs would help us to elucidate its function, if any. I determined the rate of mimicry and of species-specific vocalisations of the spotted bowerbird *Ptilonorhynchus maculatus* when alone, when in the presence of a conspecific and when in the presence of a human. Mimetic rate was low and highly variable in all contexts but did increase in the presence of heterospecifics (humans). The proportion of mimicry that comprised predatory/aggressive species did not increase in the presence of a human heterospecific and there was a short duration between mimicry and species-specific hisses. Rates of species-specific vocalisations did not increase in the presence of heterospecifics but rather increased in the presence of conspecifics. These findings suggest that mimicry may function to communicate with heterospecifics, but is not deceptive.

Introduction

The function of mimicry in passerines is poorly understood (Kelley et al. 2008) and is often ascribed following a single observation of a species mimicking in a particular context. For example, a nesting female satin bowerbird *Ptilonorhynhus violaceus* mimicking a predator when disturbed at her nest has been attributed to Batesian mimicry, whereby mimicry of a predatory species is produced to deter a potential predator (Pratt 1974). Such anecdotes are often descriptions of the behaviour of a single individual and yet a functional interpretation is frequently proposed before it is clear whether those individuals also produce the same mimicry in other situations (Wilson and Scantlebury 2006; Chu 2001b; Loffredo and Borgia 1986). Observing vocalisations in a range of naturally occurring contexts and identifying those in which mimicry occurs would help us to elucidate its function, if any.

Social context can be used to investigate the function (if any) of vocal mimicry as vocal signals are used for either intraspecific communication (e.g. sexual selection and social affiliation) or interspecific communication (e.g. Batesian mimicry, deterring competitors or attracting a third species). Depending on the hypothesis, mimicry is expected to occur (or to increase in rate) in each of three social contexts (alone, in the presence of conspecifics and in the presence of heterospecifics) in different ways. If mimicry is used in a sexual context (e.g. male display), I would expect mimicry to be produced by males only and to occur in the presence of conspecifics, both males and females. Mimicry may be used by males to signal their quality to females, to attract females to their territories or to repel rival males (Coleman et al. 2007; Loffredo and Borgia 1986). On the other hand, if mimicry is used for social affiliation, both males and females should produce mimicry and production should occur or increase in the presence of conspecifics. If produced when alone but used for social affiliation, mimicry should result in conspecifics moving to join the mimic. Finally, if mimicry is used to deter predators (Batesian mimicry) or competitors or to induce mobbing by a third species, I would expect mimicry to be produced, or to increase, in the presence of these heterospecifics and that the majority of mimetic vocalisations would be of these species.

Very little is known about the relationship between the production of mimicry and that of species-specific vocalisations either in terms of the context or of the structure of the sounds themselves. Mimicry may serve to enhance the message being conveyed in the signal (for example, if heterospecific alarm calls are combined with species-specific alarm calls to induce mobbing; Goodale and Kotagama 2006a). In this case I would expect an increase in species-specific vocalisations to be associated with an increase in mimetic vocalisations in certain contexts. Alternatively mimicry may serve a unique function in the vocal repertoire in which case I would expect mimicry to occur in distinct contexts when compared to species-specific vocalisations (Ratnayake et al. 2010). The Batesian mimicry hypothesis posits that the mimic is trying to deceive the receiver as to their true identity and thus serves a different function to species-specific vocalisations. As a result I would expect that mimicry would occur in isolated bouts with long durations between mimicry and species-specific vocalisations so as to maintain the deception.

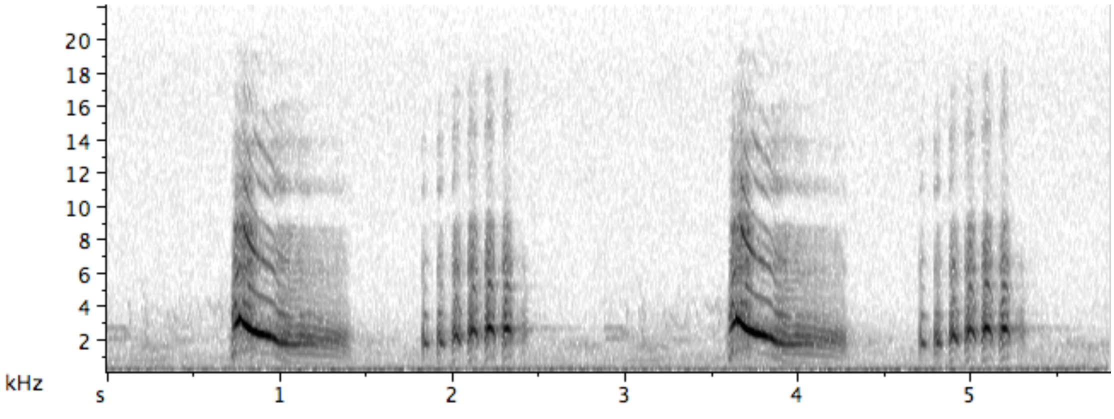
Spotted bowerbirds are Australian passerines that may mimic up to 18 bird species. They also have a small species-specific vocal repertoire mainly composed of broadband hisses, ‘advertisement’ calls, cat-like sounds and harsh churrings (Frith and Frith 2004). Male bowerbirds build and maintain bowers that are the focus of female mate choice and male rivalry (Madden 2003a). I recorded the vocalisations and behaviour of males at their bowers in three contexts: when alone, when in the presence of a conspecific, when in the presence of an avian heterospecific and when in the presence of a human heterospecific to determine whether mimicry and species-specific vocalisations occurred or increased in particular contexts. I measured the rate of mimetic and species-specific vocalisations in all contexts to address potential functions and interactions of these two types of vocalisations.

Methods

I recorded the vocalisations of 19 male bower-owning spotted bowerbirds in Taunton National Park (23.3ºS, 149.1ºE), central Queensland, Australia, in July to November 2007 and 2008. Individuals were identified by a unique series of colour bands on both legs. Males were recorded vocalising at their bowers using a Sennheiser ME66/K6 microphone and power supply onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. All recordings were carried out by an observer sitting approximately 10-15m from the bower and took place between 5:00am and 2:00pm. Recording sessions lasted between three and seven hours and the average time spent recording at each bower was 16 ± 0.95 hours (mean ± SE) per bower in 2007 and 17.13 ± 2 hours in 2008.

I recorded vocalisations of bower-owning males around the bower in three contexts: alone, in the presence of one or more conspecifics and when a heterospecific was in close proximity. Bower owners were considered to be in the presence of a conspecific whenever a bowerbird that was not the bower owner was within sight of the observer or was heard shortly after disappearing from view. A heterospecific was considered to be present when that individual was interacting either physically or vocally with the bower owner or with the bower itself. I included both avian and human interactions into the class of heterospecifics. Experimenters made visits to bowers to detail the number and type of decorations and to measure wall dimensions. These measurements were taken every 36 days in 2007 and every 33 days in 2008 (bowers were measured four times in 2007 and three times in 2008) and took approximately ten minutes (2007 average 11 minutes, 2008 average 9 minutes). All vocalisations produced by the bower owner were recorded by a second observer sat approximately 10m away.

All recordings were converted into spectrograms using Raven Pro v1.3 (Charif et al. 2004) using a Hann window and a 512 pt fast Fourier transform. I isolated and classified vocalisations into three categories: mimicry and the two most common species-specific vocalisations, hissing and ‘advertisement’ calls (Figure 1).



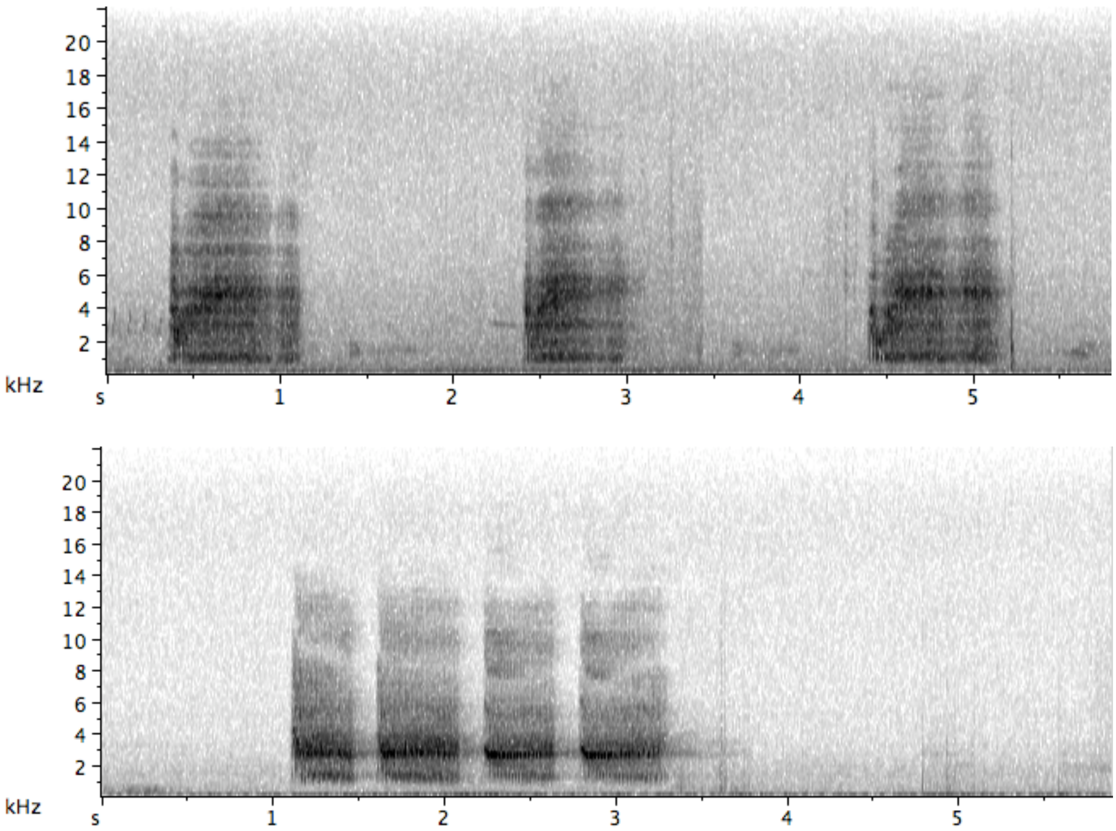


Figure 1. Spectrograms of the three main categories of bowerbird vocalisations. Top: Mimicry (of a whistling kite); middle: Hissing; bottom: An ‘advertisement’ call. Time in seconds is represented on the x-axis, frequency on the y-axis and amplitude is represented by the shade of grey/black.

Mimicry was identified by listening to recordings and visually inspecting spectrograms. Hisses were usually single harsh notes often produced in bouts and and ‘advertisement calls’ were highly distinctive calls comprising of two to four loud notes usually produced by the bower owner when perched in a tree within 10m of the bower. These sounds could be easily identified by listening to recordings. Using observational data and recordings for individual bower owners, I calculated the durations of each of the three social contexts and for each of the contexts, the proportion of time birds spent mimicking, hissing and producing ‘advertisement’ calls. To look at seasonal effects on rate of vocalisations, observations from both years were pooled and separated by date according to which month the observation was made in, and whether it was between the 1st to the 15th of that month or the 16th to the 30th/31st.

To determine whether aggressive or predatory species were over-represented during mimetic bouts, I calculated the duration of mimicry of predatory/aggressive models, competitor models and other models. I calculated the proportion of time that I would expect them to be mimicked if each model in the repertoire was mimicked for the same amount of time and calculated 95% confidence intervals from these values. I then compared these confidence intervals to the actual duration of mimicry of each type of model to determine whether certain types of models were mimicked for longer durations than predicted. I also calculated the duration between mimicry and species-specific vocalisations during disturbance events.

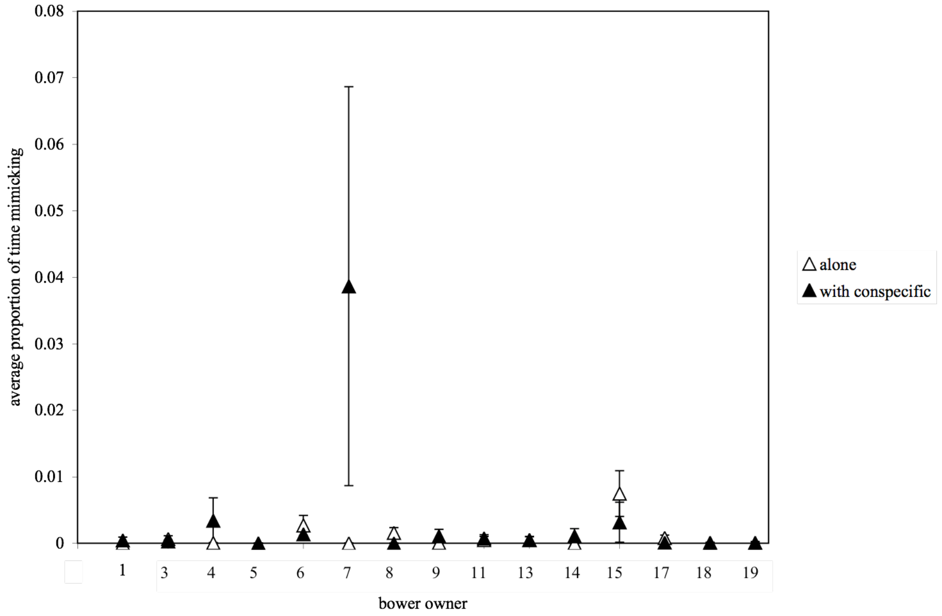
The data were manipulated and analysed using Excel, Jmp and SPSS (v. 13). All data were tested for normality in SPSS using the ratio skew: SE skew <3 (Sokal and Rohlf 1994). If normality assumptions were not met the data were transformed to normality or non-parametric tests were used. A GLM was used to test for differences in mimetic rate of individuals in different contexts.

Results

Bower owners spent as much time mimicking when they were alone as when with a conspecific (GLM; context: $F_{(1,136)} = 1.28$, $p = 0.26$; n = 15; Figure 2a) although individuals mimicked at different rates (bower owner: $F_{(14,136)} = 1.83$, $p = 0.03$). Rate of mimicry remained constant between years (year: $F_{(1,136)} = 0.07$, $p = 0.79$). The average duration between the occurrence of mimicry and the arrival of a conspecific in the bower area was 67.9 ± 12.8 minutes (mean ± SE).

Bower owners spent a larger proportion of time hissing in the presence of conspecifics than when alone (GLM; context: $F_{(1,136)} = 141.58$, $p < 0.001$; n = 17; Figure 2b). Rate of hissing did not vary with bower owner or year (bower owner: $F_{(16,136)} = 0.47$, $p = 0.96$; year: $F_{(1,136)} = 0.10$, $p = 0.75$).

(a)



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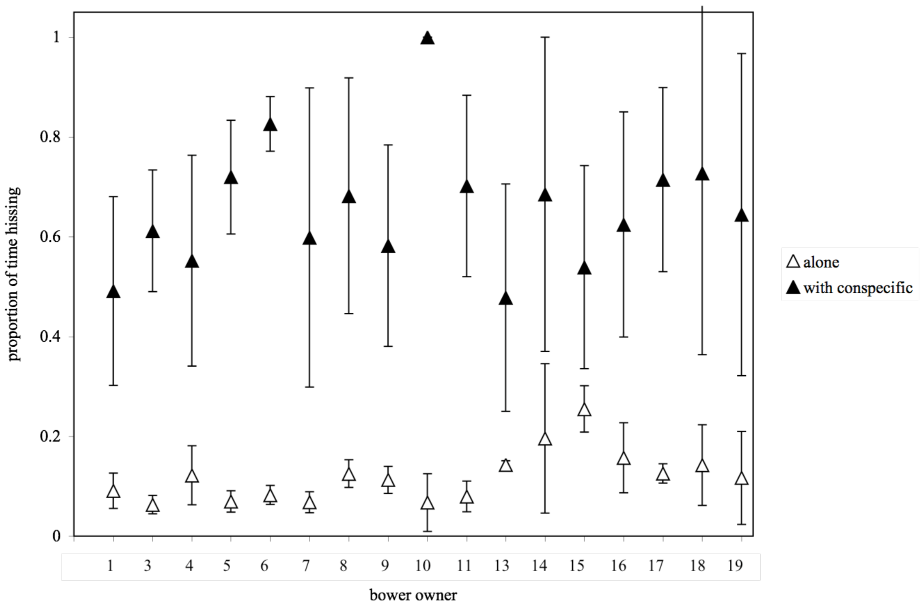
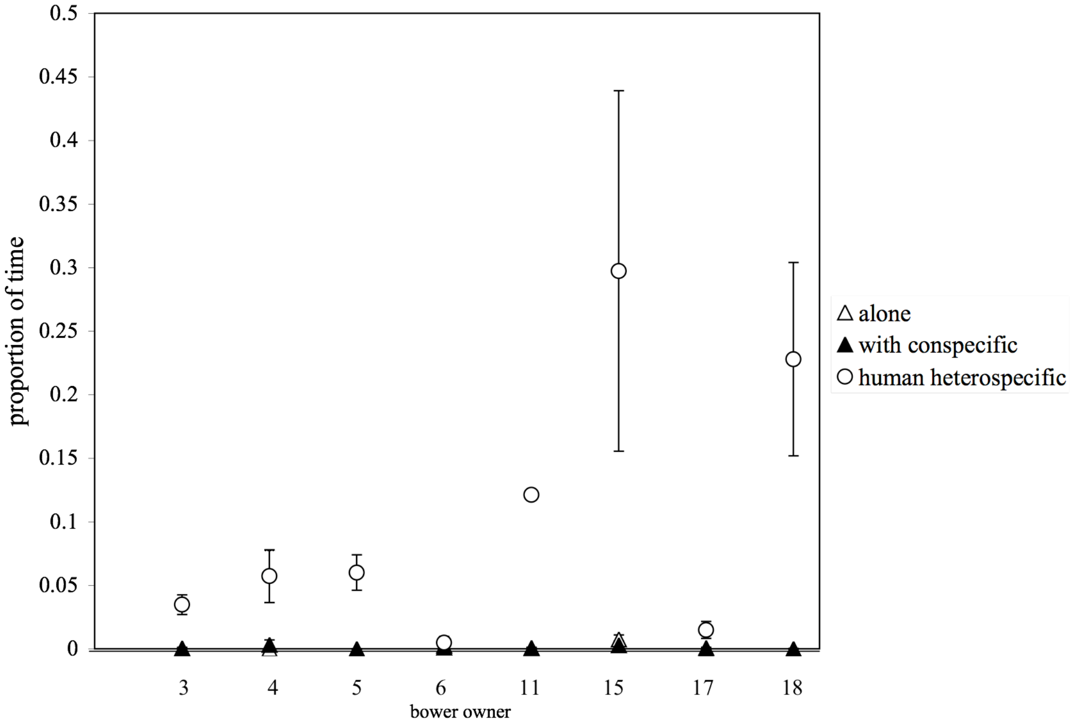


Figure 2(a). Average proportion of time (± SE) bower-owners spent mimicking alone (white triangles) and with a conspecific (black triangles) in both years combined; (b) average proportion of time (± SE) bower-owners spent hissing both years combined when alone (white triangles) and in the presence of a conspecific (black triangles).

During all observations in both years there were only three occurrences of heterospecific birds (in all cases apostlebirds *Struthidea cinerea*) directly interacting with bowers. No mimicry was observed during any of these events but the bower owners spent half (0.51 ± 0.1) of that time hissing. At a fourth bower, on a single occasion a bowerbird mimicked two species that could be heard in the background although those models were over 30m away. Mimicry was performed opportunistically in a 'duet-like' manner, with a model vocalisation being followed by bowerbird mimicry of the same vocalisation (proportion of time spent mimicking

= 0.22 ± 0.07). However, bower owners did spend a larger proportion of their time mimicking during heterospecific encounters with humans than they did when alone or when in the presence of a conspecific (GLM; context: $F_{(2,153)} = 7.28$, $p = 0.007$; bower owner: $F_{(7,153)} = 0.07$, $p = 0.79$; n = 8; Figure 3a). Males hissed more when a conspecific was present than they did when alone or when with a human heterospecific (GLM; context: $F_{(2,153)} = 147.24$, $p < 0.001$; bower owner: $F_{(7,153)} = 0.51$, $p = 0.95$; n = 8; Figure 3b).

(a)



(b)

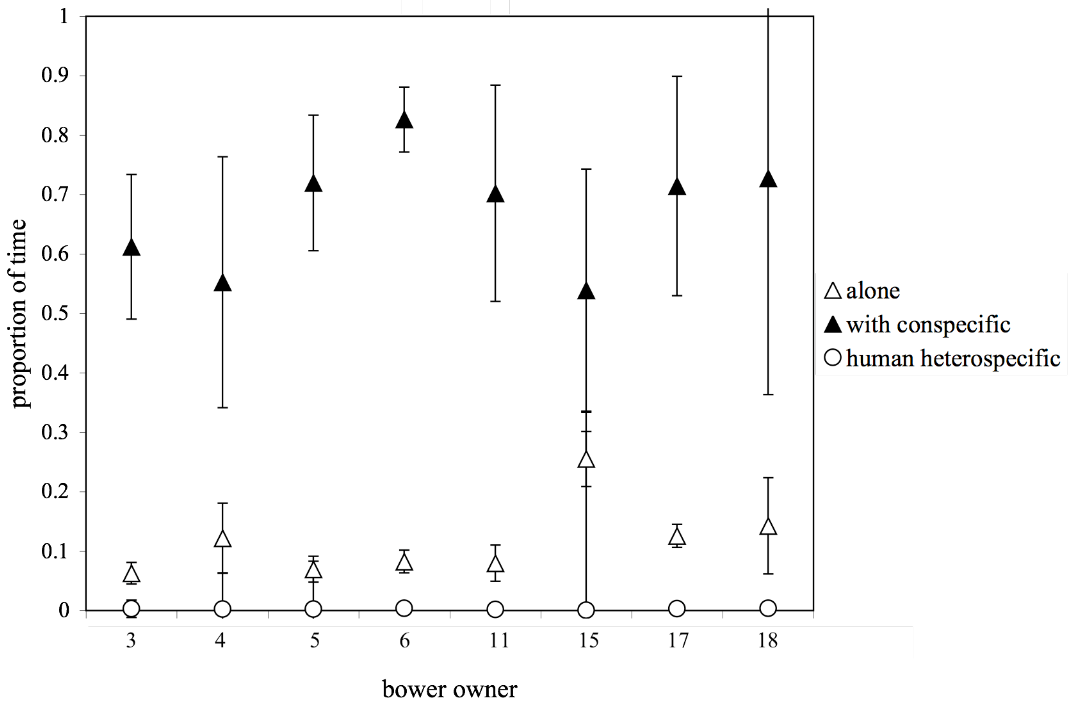
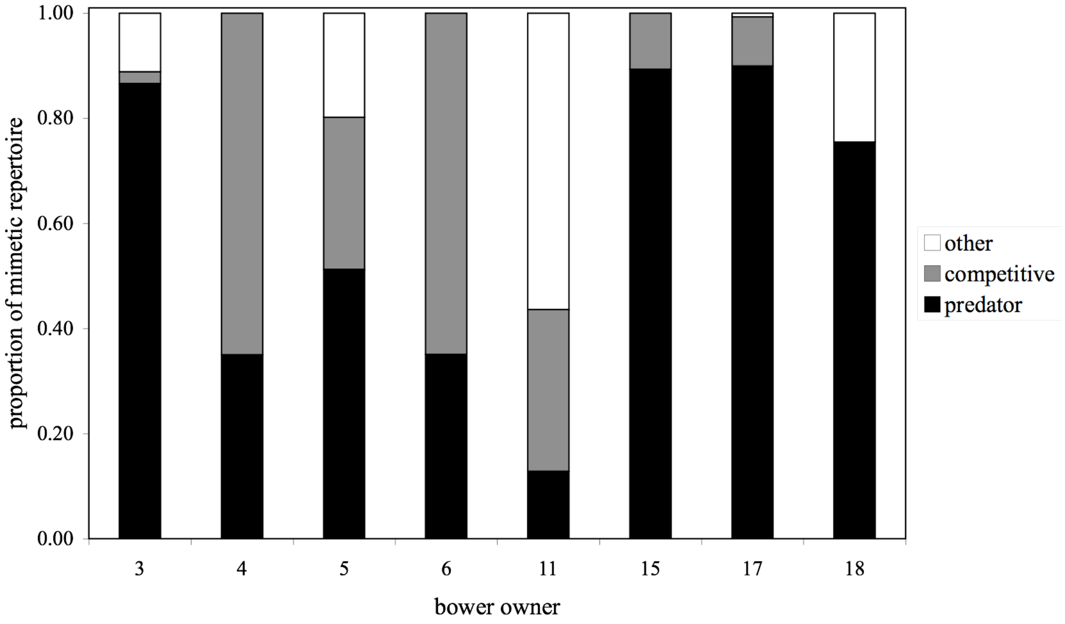


Figure 3(a). Average proportion of time (± SE) males spent mimicking when alone (white triangles), in the presence of a conspecific (black triangles) and when a human was at the bower (white circles); (b). Average proportion of time males spent hissing when alone (white triangles), in the presence of a conspecific (black triangles) and when a human was at the bower (white circles).

There was no difference in the duration that predatory/aggressive species were mimicked during human disturbance to the bower (Figure 4a) when compared with non-disturbance conditions ($t = -12$, $p = 0.10$, $n = 8$; Figure 4b). There was also no difference in the amount of mimicry of competitor models or other models in these contexts (competitor: $t = 5$, $p = 0.47$; other: $t = 3.5$, $p = 0.44$). The actual duration that each type of model was mimicked for was within the 95% confidence intervals calculated using the assumption that each model would be mimicked for an equal amount of time i.e. each model was mimicked for an approximately equal amount of time and the overabundance of predatory and aggressive species in mimicry is a result of more of those species being present in the repertoire. The average duration between hissing and mimicry (and vice versa) during disturbance to the bower was 4.1 ± 2 seconds (n = 9, 19 observations).

(a)



(b)

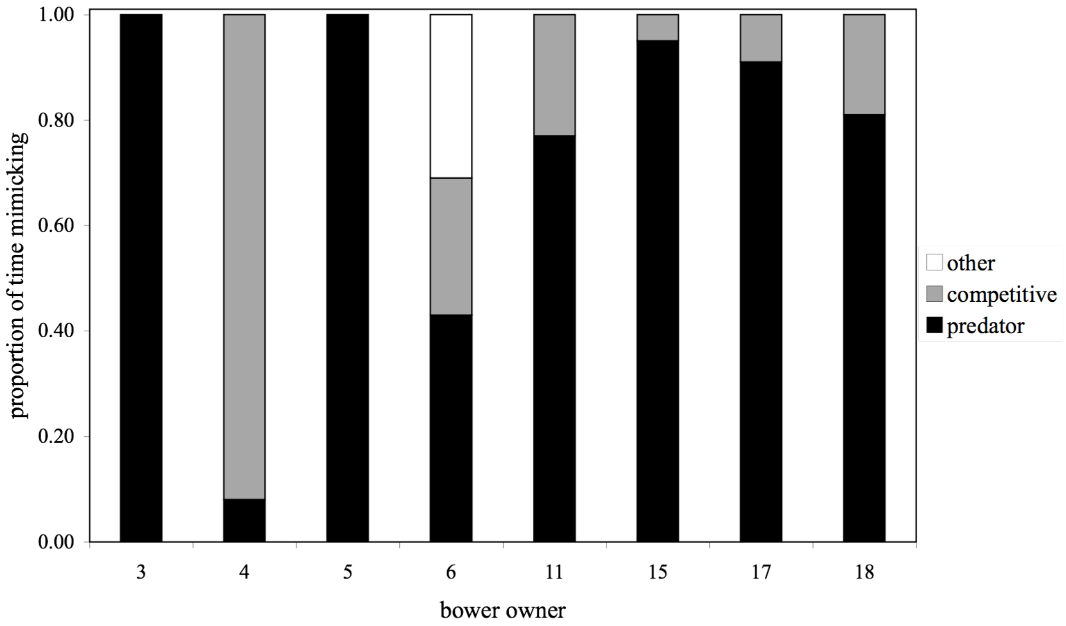


Figure 4(a) Proportion of time spent mimicking predatory/aggressive, competitor and other model species during human disturbance to the bower; n = 8; (b) Proportion of time spent mimicking predatory/aggressive, competitor and other models when males were alone at the bower or with a conspecific; n = 8.

Mimetic rate remained constant throughout the mating season (GLM: $F_{(5,127)} = 0.49$, $p = 0.49$, n = 18) but rates among individuals varied ($F_{(17,127)} = 42.28$, $p = 0.005$). Hiss rate decreased towards the end of the mating season (GLM: $F_{(5,127)} = 3.38$, $p = 0.01$; Figure 5) and all males spent similar amounts of time hissing ($F_{(16,127)} = 1.66$, $p = 0.087$, n = 17).

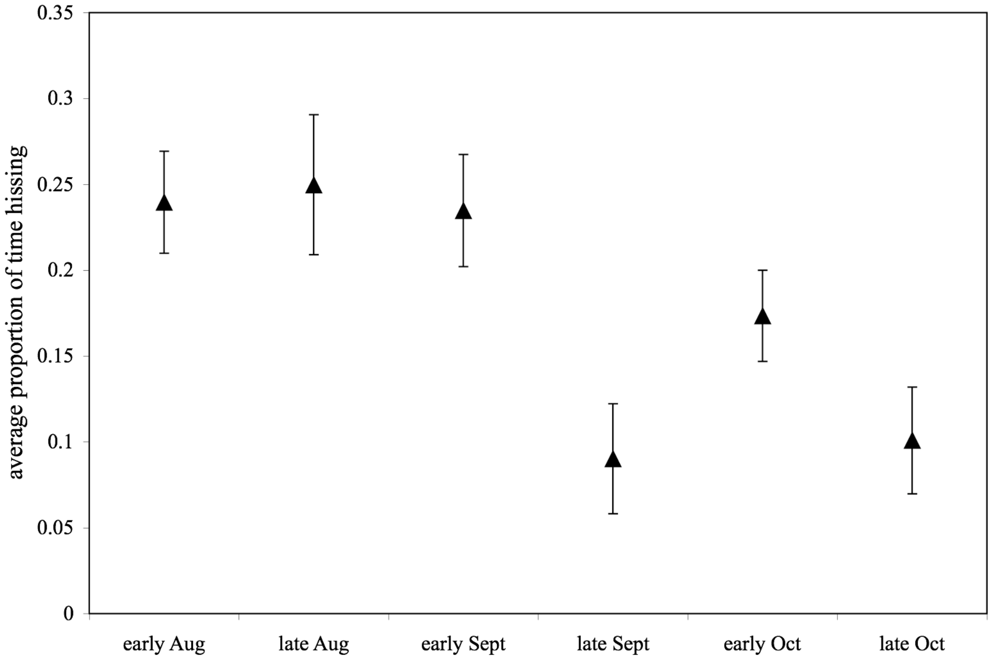


Figure 5. Average proportion of time (± SE) that males hissed at the bower in both years combined.

Bower-owning males produced an ‘advertisement’ call in 83% of observations. 1511 out of 1532 advertisement calls (99%) were produced when alone, which was significantly more than when with a conspecific ($\chi^2 = 47.90$, $p < 0.001$). Males were never observed producing ‘advertisement’ calls when heterospecifics were present at the bower. Bower-owning males differed in the time they spent calling when alone (GLM: $F_{(16, 63)} = 4.26$, $p < 0.001$, n = 17) and rate of calling increased as the mating season progressed ($F_{(5,63)} = 12.83$, $p < 0.001$; Figure 6).

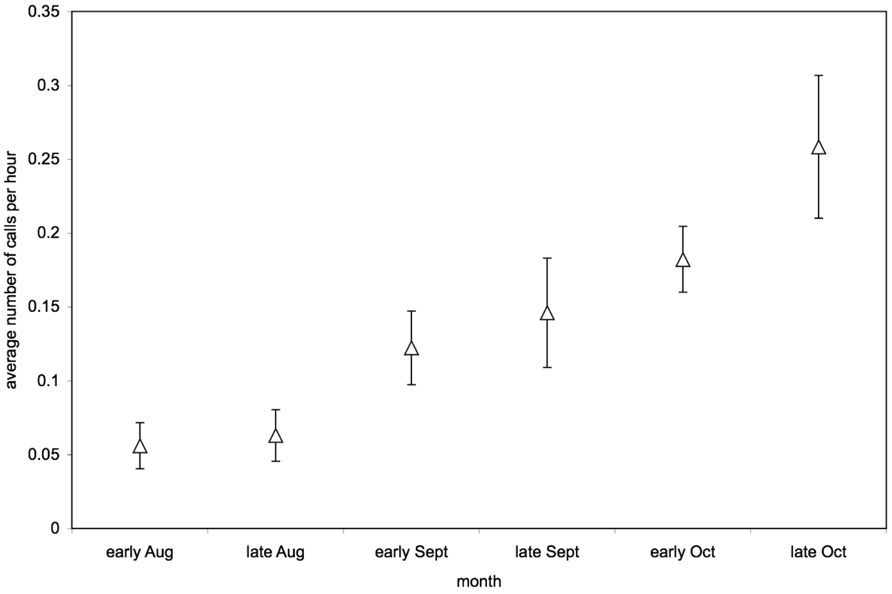


Figure 6. Average rate of ‘advertisement’ calls (calls per hour ± SE) that bower owners produced over the duration of the 2007 and 2008 field season. Months are divided into early (1st-15th) and late (16th – 30th/31st).

Discussion

When bowerbirds were alone or with conspecifics, their rate of mimicry did not differ. Bower owners responded vocally to conspecifics and avian heterospecifics by increasing their hiss rate rather than by producing mimicry. Mimetic rate did change when humans visited the bower and it increased as a result. Males did not produce more mimicry of predatory and aggressive species than predicted and the average duration between mimicry and hissing was approximately 4 seconds. Although individuals varied in the amount of mimicry they produced, the overall rate of mimicry remained the same throughout the mating season whereas hiss rate decreased. The rate of ‘advertisement’ calling also differed among males but they all increased their calling rate as the mating season progressed.

None of the observations were consistent with the hypothesis that mimicry serves an intraspecific communicative function. If mimicry was used either for sexual selection or for intraspecific communication more generally, I would have expected mimicry to occur in the presence of conspecifics or possibly to attract conspecifics to the bower, neither of which was the case (Loffredo and Borgia 1986; Robinson and Curtis 1996). Hissing appears to act as the vocalisation for communicating with conspecifics as it did change with presence of conspecifics in the expected manner. Males increased their rate of 'advertisement' calling both when alone at the bower and as conspecific presence decreased towards the end of the mating season, which is consistent with the birds using 'advertisement' calls to communicate with conspecifics. They may function by either advertising bower location to females or by maintaining territorial boundaries with rival males, although I cannot distinguish between these hypotheses here. Playback experiments would be needed to confirm whether these vocalisations are directed at males or females.

It appears, however, that bowerbirds may use mimicry to communicate with heterospecifics. Although the rate of mimicry did not change when avian heterospecifics were at the bower (but there were only three instances in the two years), it did increase when a human visited the bower. It is difficult to determine whether this is a response to humans specifically or to heterospecifics more generally given the rarity of non-human heterospecifics at the bower. Males were never observed mimicking during other interactions with humans such as capture in mist nets or walk-in traps and handling during ringing or blood sampling, which suggests that close proximity to the bower and/or decorations is required. It seems plausible that it is a general response to bower disturbance as the bowers at Taunton were rarely visited by humans. To confirm that this is the case one would need data on the vocal responses of bower owners to heterospecifics interacting with the bower itself and I have too few data to do this. If it is the novelty of human disturbance rather than disturbance itself, one might expect habituation over time and decrease in production of mimicry with increasing exposures to human or other stimuli. I currently have too few data to address this.

Although males increased their mimetic rate during disturbance to the bower they did not produce more mimicry of predatory/aggressive species when compared to other contexts. The interval between mimicry and the species-specific hiss was very short, which suggests that males were not trying to deceive as to their identity. These findings imply that mimicry may not be used in a traditionally Batesian context in this species. However, mimetic rate did increase when the bower area was disturbed, so mimicry may still be used to deter heterospecifics from the bower area. There was a suggestion that males actually produced mimicry that was more variable in terms of model content during disturbance, so males may be producing an array of sounds in an attempt to confuse the receiver (Chu 2001).

I had predicted that occurrence of mimicry would be associated with context but found that it was the rate of mimicry rather than presence/absence that varied across contexts. It is important to determine the presence/absence or rate of mimicry in different contexts: Sri Lankan magpies produced mimicry on more occasions when encountering a predator (including humans) than when in other non-threatening contexts such as territorial interactions, foraging and courting (Ratnayake et al. 2010). However, mimicry was also produced occasionally in non-threatening contexts such as when contact calling with conspecifics and when flying. It has been considered that assigning a functional explanation to mimicry requires production of mimicry in only in the relevant context and that production of mimicry in other contexts is evidence against that functional explanation. Although this may be too simplistic a view it is still the case that one cannot assign a function to vocal mimicry after recording it in a single context.

It appears that it is also useful to record occurrence of species-specific vocalisations across contexts. Species-specific vocalisations can act as a ‘control’ for the possibility that birds are simply more vocal in certain contexts. For example, while greater racket-tailed drongos *Dicrurus paradiseus* appear to use mimicry to raise the alarm they also produce a lot of species-specific vocalisations (Goodale and Kotagama 2006a). When outside their usual social group of mixed species flocks, drongos increase their rate of mimicry and of species-specific vocalisations (Goodale and Kotagama 2006b). Playbacks demonstrated that recordings with mimicry were more effective at attracting heterospecifics than recordings containing only species-specific vocalisations. The association between rate of mimicry and rate of species-specific vocalisations in two different contexts suggests that mimicry produced by drongos may be used to enhance the signal conveyed by species-specific vocalisations.

I found that bowerbirds did not produce more mimicry as their species-specific rate increased. Vocal mimicry was recorded in every context and mimicry was not produced exclusively in any context. My findings suggest that mimicry is not used by spotted bowerbirds to communicate with conspecifics but that they do use it to communicate with non-avian heterospecifics, although as yet it is unclear exactly what the message is.

CHAPTER FOUR: THE ACQUISITION OF MIMICRY

This chapter is published in Biology Letters as Kelley, L. A. & Healy, S. D. (2010). Vocal mimicry in male bowerbirds: who learns from whom?, doi: 10.1098/rsbl.2010.0093, except for the addition of Figure 3 and the data detailing human mimicry.

I collected and analysed the data and James Nicholls provided advice on analysis. I then wrote the manuscript in collaboration with S. D. Healy.

Summary

Vocal mimicry is one of the more striking aspects of avian vocalisation and is widespread across songbirds. However, little is known about how mimics acquire heterospecific and environmental sounds. I investigated geographic and individual variation in the mimetic repertoires of males of a proficient mimic, the spotted bowerbird *Ptilonorhynchus maculatus*. Male bower owners shared more of their mimetic repertoires with neighbouring bower owners than with more distant males. However, inter-bower distance did not explain variation in the highly repeatable renditions given by bower owners of two commonly mimicked species. From the similarity between model and mimic vocalisations and the patterns of repertoire sharing among males, I suggest that the bowerbirds are learning their mimetic repertoire from heterospecifics and not from each other.

Introduction

Songbirds typically learn their species-specific vocalisations as juveniles or young adults from conspecifics. However, approximately 20% of species also incorporate non-species specific sounds into their song repertoires. Despite these impressive displays of learning and vocal production, the acquisition and the function of such mimicry remains unclear (Kelley et al. 2008). Although frequently assumed to serve some functional benefit to the mimic, it is plausible that songbirds acquire vocalisations from heterospecifics simply due to some degree of imprecision in the process by which they learn vocalisations from conspecifics. Alternatively, individuals may deliberately learn sounds from their environment if mimicry serves a particular function, such as mimicking predators for defence (Dobkin 1979). Similarly, mimics may learn from their acoustic environment if the 'accuracy' of mimicry functions as an indicator of male age or quality e.g. in sexual selection (Zann and Dunstan 2008; Coleman et al. 2007). One way to investigate the acquisition and function of mimicry is to determine the entirety of an individual's mimetic repertoire to examine how this repertoire relates to possible sound sources. To my knowledge, this has never been done in the wild.

Although better known for their bower building and bower decoration skills (e.g. Frith and Frith 2004), spotted bowerbirds *Ptilonorhynchus maculatus* are also proficient vocal mimics, typically mimicking over a dozen heterospecifics and other environmental noises. Males build bowers at least 1km apart, far enough that they may not be able to hear each other's vocalisations when at their own bowers. However, they regularly visit each other's bowers to steal decorations and to destroy the bower. Such raids are usually directed at nearby bowers rather than those further away and thus the rate of bower-owning males' interactions with other bower owners is related to the distances between their bowers (Madden et al. 2004). As territorial songbirds often share their repertoires with neighbouring males (e.g. Nicholson et al. 2007), it seems plausible that the mimetic repertoires of bower owners would also be more similar the closer the neighbour. Mimetic repertoire sharing might come about in several ways, which may relate to function (if any): (1) birds mimic each others' vocalisations, either deliberately or due to imperfect learning; (2) birds mimic heterospecifics in their environment (Kaplan 1999), which are likely to be similar species when bowers are closer together.

Here I attempt to distinguish between these two alternatives by examining mimetic repertoire sharing among male spotted bowerbirds and the detailed structure of mimicry of two commonly mimicked models: the pied butcherbird *Cracticus nigrogularis* and the whistling kite *Haliastur sphenurus*. Whilst acquisition from conspecifics or heterospecifics may both lead to local repertoire sharing, males learning directly from heterospecifics should demonstrate repeatable individual differences in renditions of their mimicry, whereas if males learn from each other, I would expect males to have both similar repertoires and renditions of mimicry.

Methods

I recorded mimicry of 19 male bower-owning spotted bowerbirds in Taunton National Park (23.3ºS, 149.1ºE), central Queensland, Australia, during 2007 and 2008. Individuals were identified by a unique series of colour bands on both legs. Males were recorded vocalising at their bowers using a Sennheiser ME66/K6 microphone and power supply onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. Sampling effort was evenly distributed among bowers (time per bower per year 16.5 ± 1.5 hours, mean ± SE). Distances among bowers were measured using GPS co-ordinates, which were later converted into kilometres, rounded to the nearest 10 metres.

Recordings were converted into spectrograms using Raven Pro v1.3 (Charif et al. 2004) using a Hann window and a 512 pt fast Fourier transform. Mimicry was identified by listening to recordings and visually inspecting spectrograms. Song sharing between males was calculated using the number of model species a focal male shared with a particular bower owner, expressed as a proportion of the focal male's total repertoire. Mantel tests were used to test correlations between the proportion of repertoire shared and inter-bower distance in 2007 and 2008 separately, using 10 000 iterations on a full matrix without diagonals (Liedloff 1999).

I used recordings of pied butcherbird and whistling kite mimicry to investigate individual differences in production of mimetic vocalisations. I recorded from five to 10 recordings of butcherbird mimicry from each of 10 males and from two to 47 recordings of kite mimicry from each of five males. Spectrograms of these recordings were measured for start frequency, end frequency, minimum frequency, maximum frequency, peak frequency (frequency at the largest amplitude), duration and the time to maximum, minimum and peak frequency. I calculated the proportion of time to the minimum, maximum and peak frequencies, the ratios of the maximum frequency to peak frequency and frequency range, the ratios of the start frequency to end, peak and maximum frequency, the ratio of the peak frequency to frequency range and, for butcherbird mimicry, expressed the duration of the upward sweep at the end as a proportion of overall duration. Measurements that were highly correlated with other variables ($r > 0.7$) were dropped from further analyses.

Analyses of butcherbird and kite mimicry were carried out separately and discriminant function analysis was used to identify temporal or frequency measurements that classified individual bowerbird mimicry of each model. Means for each individual in canonical space were represented by group centroids and the squared Mahalanobis distances between each group centroid were used as a measurement of acoustic similarity between individuals. Matrices of these values and inter-bower distances were then used in a Mantel test to assess whether the mimicry of individuals with bowers closer together shared greater structural similarity than did individuals with bowers further apart. The repeatability (intra-class correlation coefficient) of the parameter that accounted for the most variation in mimetic production for each species was calculated based on among and within male variance components derived from a one-way ANOVA (Lessells and Boag 1987). Unless stated otherwise, all analyses were carried out using JMP (Version 7).

Results

I identified mimicry of 16 different species of heterospecific, including one example of human imitation. The average repertoire size of bower-owning males in 2007 was 3.7 ± 0.5 models and in 2008 was 3.2 ± 2.6 (range 0-8, both years). The average nearest-neighbour distance among bowers was 1740 ± 700 m (range 880 – 2830 m). In both years, males shared a larger proportion of their repertoire with males whose bowers were closer to their own bower than they did with males who had bowers further away (Mantel test: 2007: 17 x 17, r = 0.246, $p < 0.001$; 2008: 13 x 13, r = 0.355, $p < 0.001$; Figure 1).

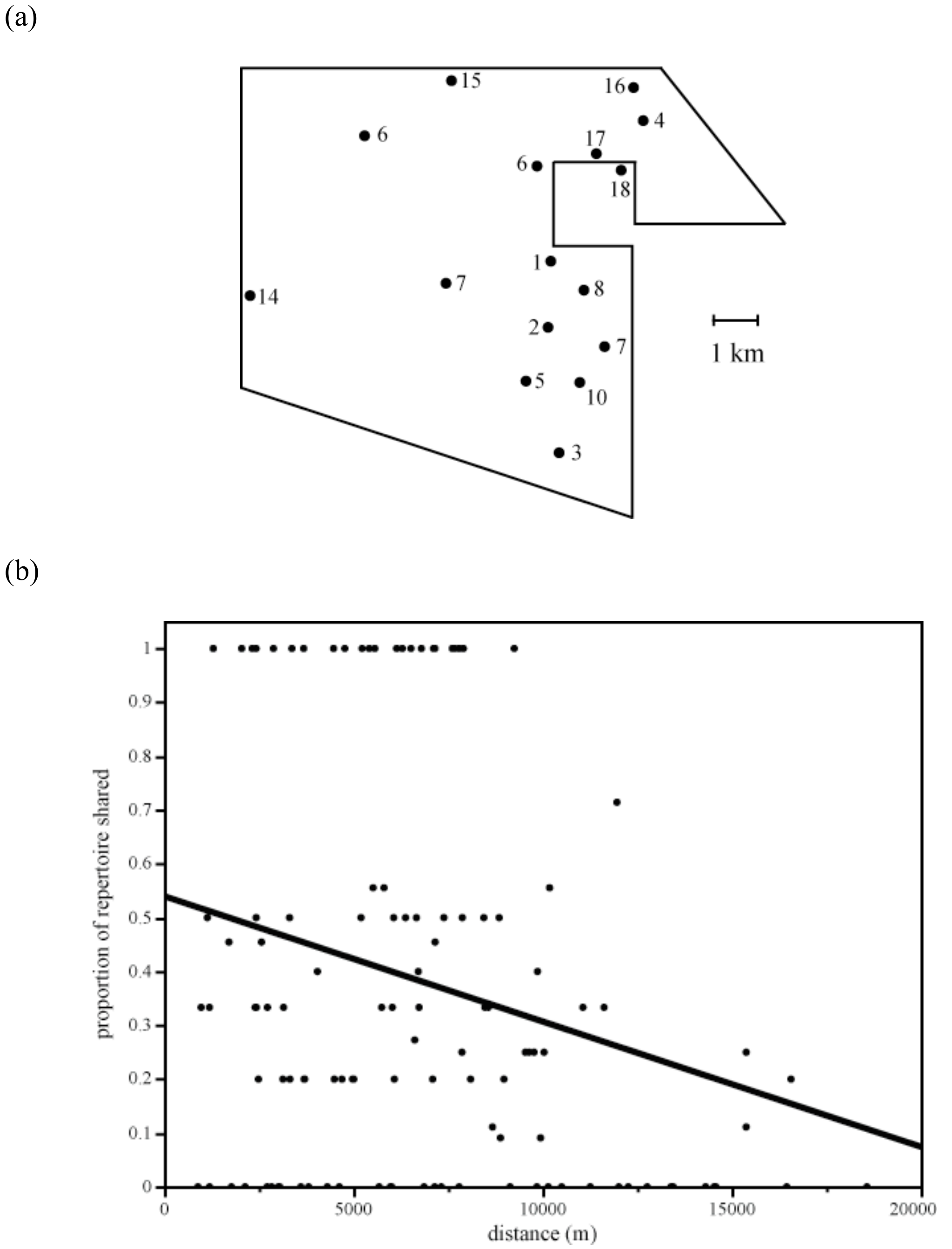


Figure 1(a) Map of Taunton National Park showing the distribution of bower sites, represented by numbered dots. Bower 12 and 19 (used in 2007 analysis only) and bower 13 (used in 2008 only) are not shown and are 7.9 km, 5.1 km and 9.4 km respectively outside the park boundary; (b) The proportion of repertoire shared against inter-bower distance for all pairs of males in 2007. The solid line represents best fit.

Discriminant function analysis revealed individual differences among renditions of pied butcherbird mimicry (Wilks' $\lambda = 0.023$, $F_{9,70} = 6.96$, $p < 0.0001$; Figure 2) and whistling kite mimicry (Wilks' $\lambda = 0.26$, $F_{4,53} = 4.13$, $p < 0.0001$, Figure 3). For pied butcherbird mimicry, the first two canonical roots had eigenvalues greater than 1 and contributed over 76% of the discriminatory power. The structural measurements that contributed most to the discriminant functions were duration, start frequency, end frequency, ratio of start frequency to maximum frequency, and the proportion of time to maximum frequency. For whistling kite mimicry, the first canonical root had an eigenvalue greater than 1 and contributed over 86% of the discriminatory power. The temporal and spectral measurements that contributed most to the discriminant functions were the ratio between start and end frequency, minimum frequency, frequency range and the ratio of peak to maximum frequency.

A Mantel test using group centroids and inter-bower distance matrices revealed that there was no relationship between the measured acoustic characteristics of mimicry and distance between bowers for either butcherbird or kite mimicry (butcherbird: 10 x10, $r = -0.13$, $p = 0.71$, $n = 10$; kite: 5 x 5, $r = 0.495$, $p = 0.15$, $n = 5$). Repeatability analyses on the measurement that explained the most variation in mimetic structure revealed that these vocalisations were highly repeatable within individuals (butcherbird, duration r = 0.79; kite, ratio of start to end frequency r = 0.42).

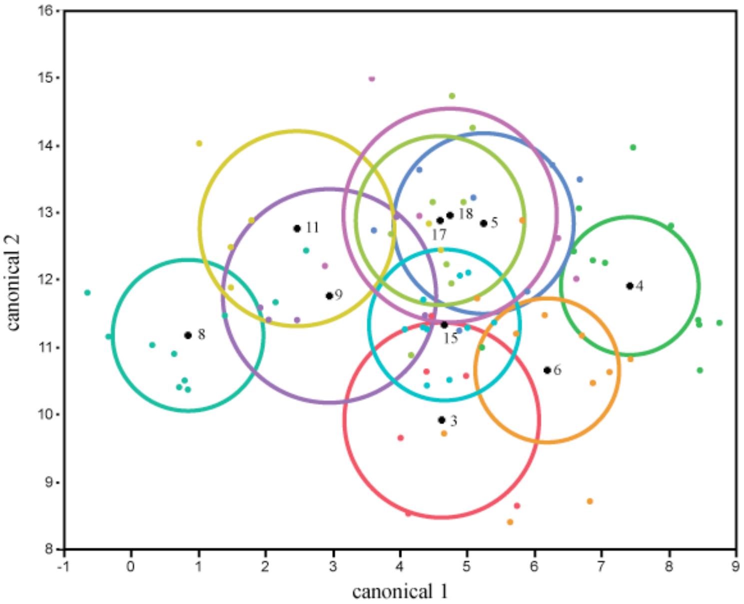


Figure 2. Discriminant analysis of pied butcherbird mimicry. Each point represents one mimetic recording and each colour represents a different individual. Circles are 95% confidence intervals for each individual's mean centroid value (individuals numbered 1 – 10). Non-intersecting circles indicate individuals produced significantly different mimetic sounds.

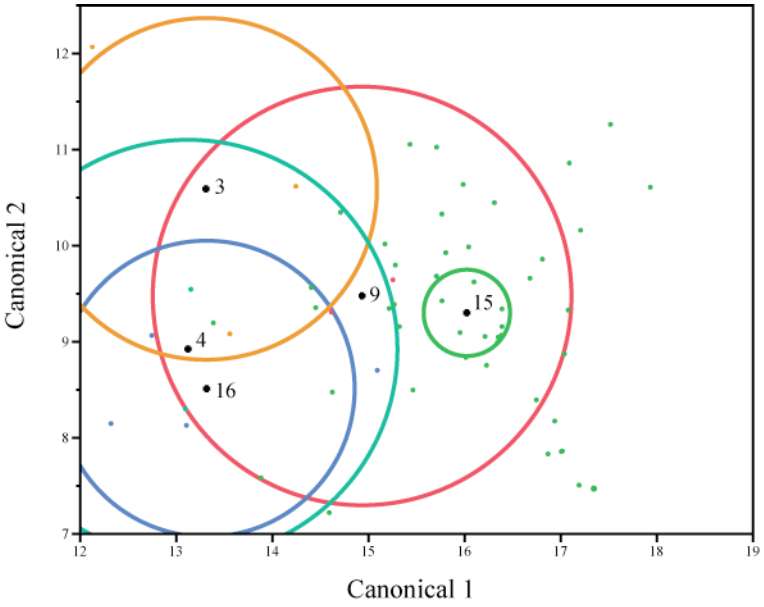


Figure 3. Discriminant analysis of whistling kite mimicry. Each point represents one mimetic recording and each colour represents a different individual. Circles are 95% confidence intervals for each individual's mean centroid value (individuals numbered). Non-intersecting circles indicate individuals produced significantly different mimetic sounds.

Two bowerbirds with territories outside Taunton were recorded mimicking a human voice. A male that owned bower 12 in 2003 but subsequently lost his bower to another male was recorded producing mimicry of a human voice in 2007 (Figure 4) and 2008. In 2007 I also recorded at least one unbanded male mimicking the same vocalisation. The model vocalisation being mimicked was from a human female calling for her pet cat, Bonnie. This 'Bonnie' call was given daily and was shouted loudly by the same person approximately 300 metres from bower 12.

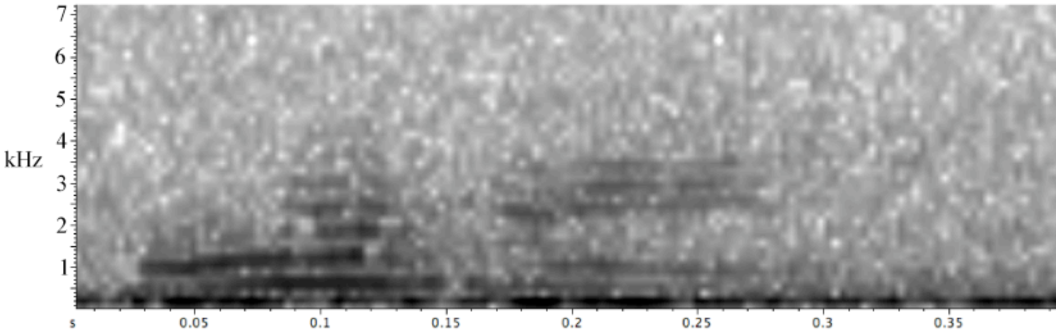


Figure 4. Spectrogram of a male bowerbird mimicking the word ‘Bonnie’. Time in seconds is represented on the x-axis, frequency in kHz on the y-axis and amplitude is represented by the shade of grey/black.

Discussion

Males with bowers closer together had more similar mimetic repertoires than did males with bowers further apart. However, variation in the reproductions of the sounds of two of the most commonly mimicked species was not explained by inter-bower distance. Moreover, individuals were highly repeatable in aspects of these vocalisations.

My finding that males were more likely to share the contents of their repertoire the closer they were to another bower owner is consistent with the birds learning either from conspecifics or heterospecifics. However, closer inspection of two of these shared sounds shows that the detailed structures of the mimicry were not explained by spatial proximity. Instead, the high among-male variability in butcherbird and kite mimetic structure suggests that learning directly from heterospecific models is more likely. However, it is also important to consider how accurately males learn their mimicry, as our findings may also be explained in terms of imperfect copying i.e. if males copy vocalisations inaccurately neighbouring males would also have structurally dissimilar mimicry.

I found conclusive evidence that males can learn directly from heterospecifics, as at least two bowerbirds mimicked a human vocalisation. This also provides evidence that bowerbirds can learn mimetic sounds as adults as the banded ex-bower owner was at least five years old when it first mimicked this vocalisation. This vocalisation was also incorporated into the mimetic repertoire of at least two birds in under a year. The vocalisation being mimicked had been present in the acoustic environment for a year as the cat Bonnie that was being called was only a year old.

To my knowledge, the only other study on vocal mimicry to examine geographic variation in structure across mimics is one on Albert's lyrebird males *Menura alberti*. They also appear to learn their mimicry directly from a heterospecific (satin bowerbirds *Ptilonorhynchus violaceus*) as geographically discrete populations of male lyrebirds faithfully reproduce the structurally distinct songs of the corresponding local population of satin bowerbirds (Putland et al. 2006). Unlike the spotted bowerbirds, there is less variation in the structure of mimicry within populations of lyrebirds than there is in the structure of the vocalisations of the local satin bowerbird models. This may mean lyrebirds may copy each other and not models directly. It seems likely that a spatial analysis of content and mimetic structure would determine if this was the case.

Birds copying the vocalisations of heterospecifics provide some of the most striking examples of animal mimicry, yet we know remarkably little about its adaptive significance, if any. Tests of sexual selection on repertoire size, or vocal mimicry as a defensive adaptation have proved equivocal at best (as reviewed in Kelley et al. 2008). Moreover, in stark contrast to more conventional song learning in birds (e.g. Catchpole and Slater 2008), we know next to nothing about how vocal mimicry develops mechanistically. Here, I have at least begun the process of studying both mechanism and function by identifying the likely models for, and the sources of variation in, spotted bowerbird vocal mimicry.

CHAPTER FIVE: GEOGRAPHIC VARIATION IN VOCALISATIONS

I collected and analysed the data and wrote the first draft of this chapter, which was then completed in collaboration with S. D. Healy.

Summary

To determine what governs the choice of models made by a vocal mimic I surveyed the mimetic repertoire of three geographically isolated populations of spotted bowerbird *Ptilonorhynchus maculatus*. Model choice across these sites (which were between 200km and 600km apart) overlapped significantly and the majority of mimetic repertoires at each site were composed of the vocalisations of aggressive species. These findings suggest that mimicry may function to deter heterospecifics. On closer inspection of the structure of two sounds that were mimicked I found that males did not produce site-specific renditions of mimicry. The species-specific hiss was also not site specific although the birds did produce site-distinctive ‘advertisement’ calls that were also individually distinctive within populations.

Introduction

Little is known as to why a mimetic species copies particular sounds in its environment. Directly determining why a species mimics particular sounds can be difficult but useful contributions can be made using correlational analyses. For example, if a species that mimics has a wide geographic distribution, examination of the models mimicked as the distribution of models (and therefore the acoustic environment) changes may allow determination of the function of such mimicry. If birds simply mimic the most common species in their acoustic environment, I would expect repertoire composition to change as the acoustic environment changes, which it is likely to do as the distance between mimics increases. However, if the mimics copy a particular subset of sounds in the environment (for example, producing copies of the vocalisations of predators if mimicry is used to intimidate conspecifics or heterospecifics) then, as distance increases, I would expect mimics in geographically isolated populations to mimic the same kind of subset (for example, the local predators).

At Taunton National Park in Australia, the preference for mimicking aggressive species by male spotted bowerbirds *Ptilonorhynchus maculatus* (Chapter 2) may be explained by mimicry being used in a Batesian context to deter con- or heterospecifics (where vocalisations of predatory or aggressive species are preferentially mimicked; Dobkin 1979; Harcus 1977). Alternatively, these sounds may be mimicked due to their structural properties as these calls are also characterised by their relative simplicity and loudness (Hindmarsh 1984). I attempted to distinguish between these explanations by using the composition of the mimetic repertoires of male spotted bowerbirds at two further sites geographically isolated from both Taunton and each other. I did this in two ways: (1) by categorising mimicked sounds at each site into predatory, aggressive, competitor or other species; and (2) examining the structure of mimicked sounds.

Detailed examination of the mimetic repertoires of bowerbirds at Taunton revealed that males with bowers closer together had more similar mimetic repertoires than did males with bowers further apart (Chapter 4; Kelley and Healy 2010). This spatial relationship among males suggested that mimetic sounds may be learned from neighbouring bowerbirds or directly from the model species (as males with bowers closer together are more likely to share similar acoustic environments and hence mimic the same models). Closer examination of two aggressive models commonly mimicked at Taunton revealed that bower owners gave individually distinct renditions of those models: the pied butcherbird *Cracticus nigrogularis* and the whistling kite *Haliastur sphenurus* vocalisations. These vocalisations were not more similar among neighbouring male bower owners when compared to non-neighbouring males. This suggests that mimicry is not learned from neighbouring bowerbirds but from model species in the environment.

Confirmation of this would be provided by evidence that male spotted bowerbirds in geographically isolated populations mimicked the vocalisations of local species. If mimicry is used in a Batesian context, I would expect the vocalisations of predators or aggressive species that were found at each site to be mimicked. I would also expect mimicked sounds to reflect any local variation in the structure of model sounds. Geographic variation in the structure of songbird vocalisations is well documented (e.g. Catchpole and Slater 2008) and if any of the model vocalisations that are mimicked vary in this way then this variation should be reflected in the structure of bowerbird mimicry. I would therefore expect there to be variation in renditions of mimicry given by bowerbirds at different sites. Recording model vocalisations at different locations and comparing these sounds with those mimicked by bowerbirds at each site can confirm that mimicry is learned from local models.

Despite geographic variation in songs being well documented, little is known about how species-specific vocalisations other than song vary in different populations of a songbird species. Satin bowerbirds *Ptilonorhynchus violaceus* produce ‘advertisement’ calls that vary with habitat type as these vocalisations are adapted to enhance transmission in different environments (Nicholls 2008; Morton 1975). Spotted bowerbirds produce a similar call and therefore I would expect males in different habitats to produce structurally distinct ‘advertisement’ calls. To test this, I recorded ‘advertisement’ calls from male bower owners at three sites. Two of these sites comprised fairly open habitats and one site contained more mature dense woodland. I predicted that male bower owners in the dense habitat would produce ‘advertisement’ calls that had lower frequencies than those produced by males in the more open habitats, as sounds with lower frequencies are transmitted more efficiently through dense environments (Nicholls and Goldizen 2006). Another species-specific vocalisation, the hiss, is commonly produced by bowerbirds when in the presence of a conspecific (Chapter 3). As these are short-range signals compared to ‘advertisement’ calls, these vocalisations are unlikely to be shaped by the habitat in the same way. It is unknown whether these vocalisations vary within or among individuals. If either ‘advertisement’ calls or hisses vary on a small scale (for example, within sites) then these vocalisations may be used for individual identification. In this case I would expect bower owners to produce vocalisations that have an individually distinctive structure and that are highly repeatable within individuals.

Methods

I recorded the vocalisations of male bower-owning spotted bowerbirds in three sites in central Queensland between July and November 2007 and 2008: Taunton National Park, Idalia National Park and Brigalow Research Station. Taunton National Park (23.3ºS, 149.1ºE) is approximately 250km west of Rockhampton (Figure 1). It covers approximately 11,470 hectares of mixed woodland and brigalow *Acacia harpophylla* where I found 18 bowers in 2007 and 14 in 2008. Bower owners at this site were identified by a unique series of colour bands on both legs. The average time spent recording at each bower was 16 ± 0.95 hours (mean ± SE) per bower in 2007 and 17.13 ± 2 hours in 2008. The second site was Idalia National Park (24.9ºS, 144.7ºE), which is approximately 100km southwest of Blackall and approximately 450km SW of Taunton National Park (Figure 1). It covers an area of 140,000 hectares comprising brigalow and mixed woodland and four bowers were found at Idalia in both years. 21 hours of recordings were taken at each bower in 2007 and 21.75 ± 5.6 hours in 2008. The third site was Brigalow Research Station (24.5ºS, 149.5ºE), which is situated approximately 70km SW of Biloela (Figure 1) and approximately 250 km southeast of Taunton. It covers 4,250 hectares of pasture with patches of native vegetation, predominantly brigalow and five bowers were found in 2007. 9.9 ± 1.4 hours of recordings were taken at each bower in 2007. Four of these bowers and one new bower were found in 2008 and recordings were taken at each bower for 12.7 ± 1.7 hours. Bower owners at Idalia and Brigalow were not banded.

The three sites differed predominantly in terms of canopy coverage and forest density: Taunton comprised mainly of dense brigalow regrowth, Idalia was quite exposed and had large cleared areas alongside mature woodland and Brigalow had large pastures bordered by mature woodland.

Figure 1. Map of central Queensland showing the location of Idalia National Park, Brigalow Research Station and Taunton National Park.

Males were recorded vocalising at their bowers using a Sennheiser ME66/K6 microphone onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. All recordings were carried out approximately 10-15m from the bower and took place between 5:00am and 5:00pm. Mimicry was identified by listening to recordings and visually inspecting spectrograms of suspected mimicry. These were then compared against model recordings, spectrograms from models recorded at all three locations and from the Simpson & Day (1999) CD-ROM of bird sounds for species where no model vocalisation had been recorded. Mimetic repertoire profiles were then constructed for bower owners at Taunton (using data from Chapter 2), Idalia and Brigalow in 2007 and 2008. As birds at Idalia and Brigalow were not individually identifiable the bower owner was identified as: the bowerbird that was present for the longest amount of time, that appeared to be maintaining the bower and that was observed displaying to conspecifics. Juvenile auxiliary males are usually only tolerated around the bower area when the breeding season commences in June/July (Frith and Frith 2004) so it is likely that the actual bower-owning male was identified correctly as the data were collected at these sites once the mating season had commenced (the earliest observations at these sites were in September).

I constructed mimetic repertoire profiles for bower owners at Taunton, Idalia and Brigalow using data from both years combined. These were classified as generally predatory/aggressive, competitor or other species based on the definitions in Chapter 2 and using Simpson (1999), and my classifications were again corroborated by J. A. Nicholls. The categories of generally aggressive and predatory were combined as species that were predatory were also classified as aggressive. I compiled a list of species present at each site using the Atlas of Australian Birds (an online resource that lists all birds observed within a defined area) to determine how similar the acoustic environments at each site were. Using the same categories we applied to mimicry at Taunton (as described in Chapter 2 based on Hindmarsh 1986) sounds from Idalia and Brigalow were scored for complexity in frequency structure and frequency modulation. I used these measures of complexity to determine the number of complex and simple vocalisations that were present in the vocal repertoire of males at each site.

Mimetic renditions of the pied butcherbird and whistling kite were used to test for structural differences in mimicry among sites. Bowerbirds mimicked pied butcherbirds and whistling kites at all three sites. Only one recording of pied butcherbird mimicry was obtained at Idalia so this was excluded from the analysis. Spectrograms of pied butcherbird and whistling kite recordings were measured for start frequency, end frequency, minimum frequency, maximum frequency, peak frequency, duration and the times to maximum, minimum and peak frequency. I calculated the proportion of time to the minimum, maximum and peak frequencies, the ratios of the maximum frequency to peak frequency and frequency range, the ratios of the start frequency to end, peak and maximum frequency, the ratio of the peak frequency to frequency range and, for butcherbird mimicry, expressed the duration of the upward sweep at the end as a proportion of overall duration. Measurements that were highly correlated with other variables ($r > 0.7$) were dropped from further analyses and the measurements for each individual mimic were averaged.

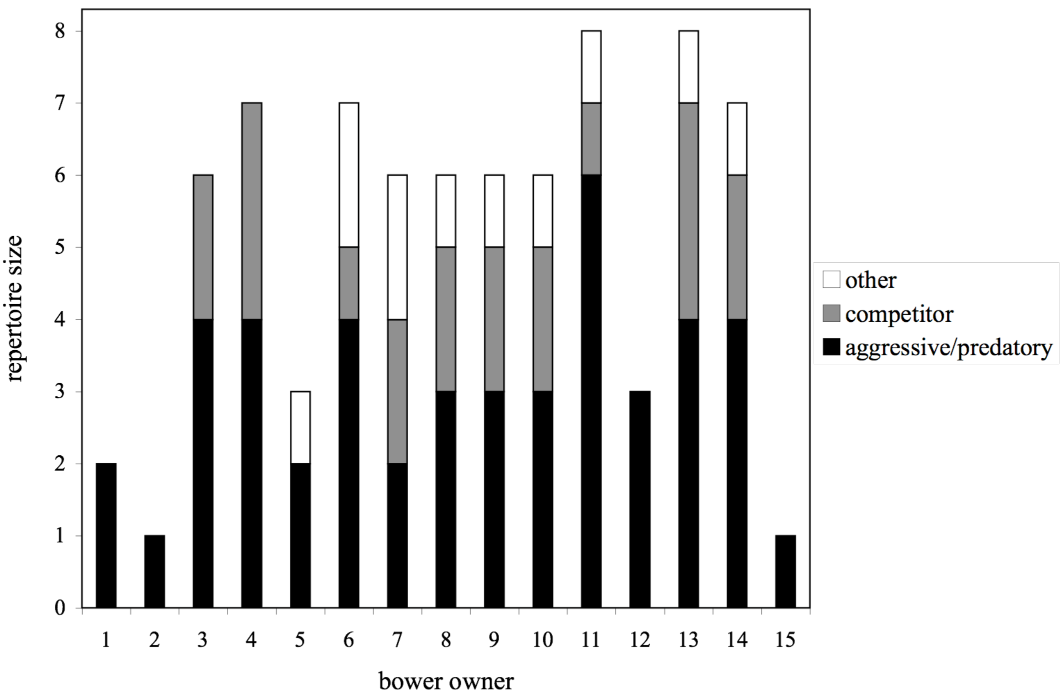
Analysis of each model was carried out separately and discriminant function analysis was used to identify temporal or frequency measurements that classified mimicry of each model at each of the three sites. Repeatability analyses were also carried out on the variable that explained the most variation in each discriminant analysis (Lessells and Boag 1987). I also applied the first two canonical scores generated from the discriminant function analysis of mimicry to model vocalisations recorded at each site to determine how similar model sounds were when compared to mimetic sounds.

Where possible I isolated recordings of ten hisses and ten 'advertisement calls' from each individual when alone at their bower at each site (when fewer than three vocalisations were recorded from an individual that individual was excluded). For recordings at Idalia and Brigalow I used recordings from one year for each bower only as I did not know if males retained their bowers between years. Each sound was then converted into a spectrogram and I measured the duration of vocalisation, peak frequency and the time at peak frequency. Frequency boundaries of hisses and 'advertisement' calls are not clearly delineated on spectrograms due to the harsh, grating nature of the sounds. A spectrogram slice of the sound was generated (Hann window, 256 samples, 50% overlay) and I measured maximum and minimum frequency 10dB below the peak of the spectrum to standardise these measurements (S. A. Zollinger, pers. comm.). Any variables that had a correlation of greater than 0.7 were excluded from further analysis and discriminant function analyses were used to test for differences within and among sites in hissing and 'advertisement' calls. Repeatability analyses were carried out on the variables that explained most of the variation in hissing and 'advertisement' calls.

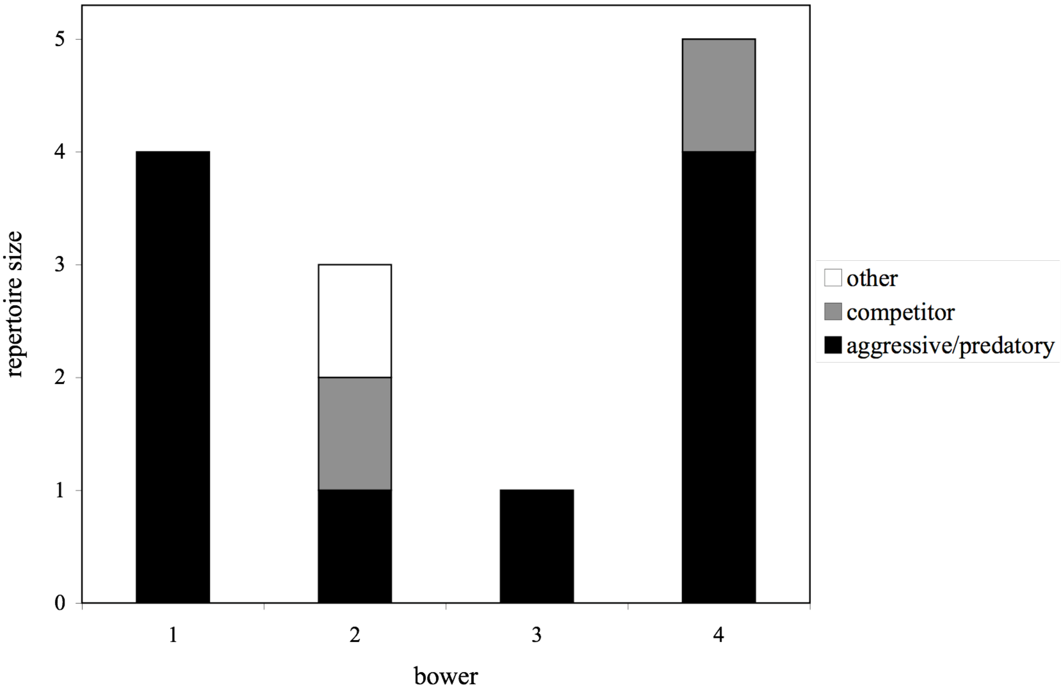
Results

Seven species of heterospecific were mimicked at all three field sites: whistling kite, pied butcherbird, white-winged chough *Corcorax melanorhamphos*, wedge-tailed eagle *Aquila audax*, laughing kookaburra *Dacelo novaeguineae*, grey-crowned babbler *Pomatostomus temporalis* and brown falcon *Falco berigora*. 48 bird species were present at all three sites and each site shared approximately 61% of species present with another site. Several species were mimicked at one site only. They included the pacific baza *Aviceda subcristata* at Taunton, crow *Corvus orru* at Idalia and figbird *Sphecotheres viridis* at Brigalow. As I found at Taunton in Chapter 2, a high percentage of mimicked sounds at Idalia and Brigalow were those of predatory or aggressive species (Taunton: 54%; Idalia: 75%, Briglow: 50%; Figure 1a - c). Similarly, most of the sounds mimicked at Idalia and Brigalow were structurally similar to those mimicked at Taunton. They had simple frequency modulation (Taunton: 85%; Idalia: 88%; Brigalow: 85%) and multiple frequency bands (Taunton: 69%; Idalia: 63%; Brigalow: 62%).

(a)



(b)


repertoire size
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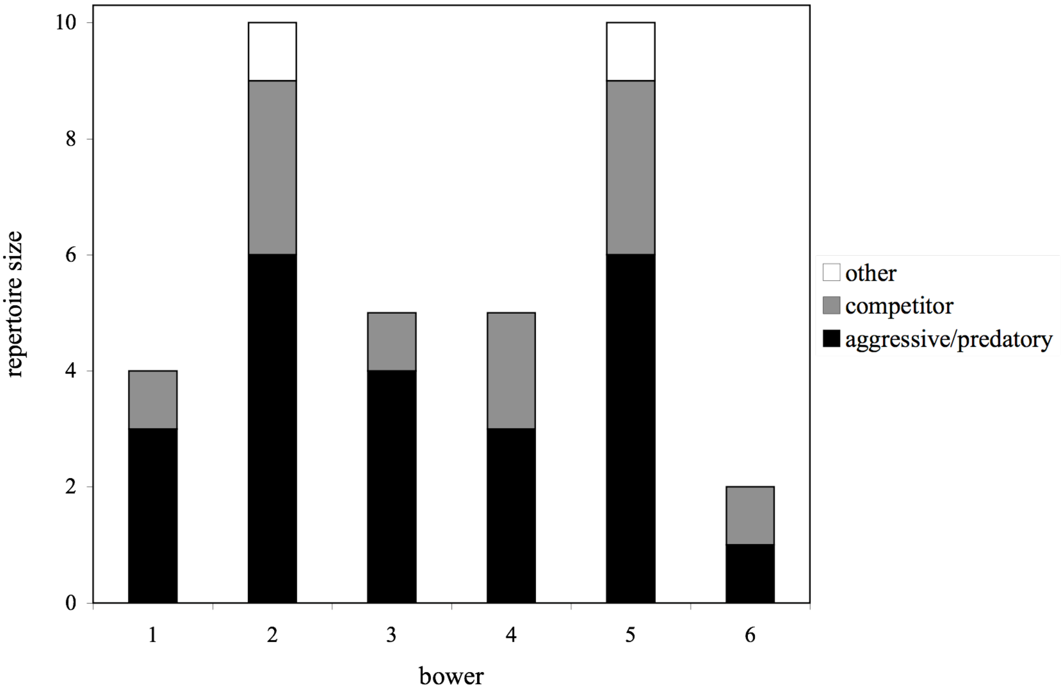
aggressive/predatory

(c)


repertoire size
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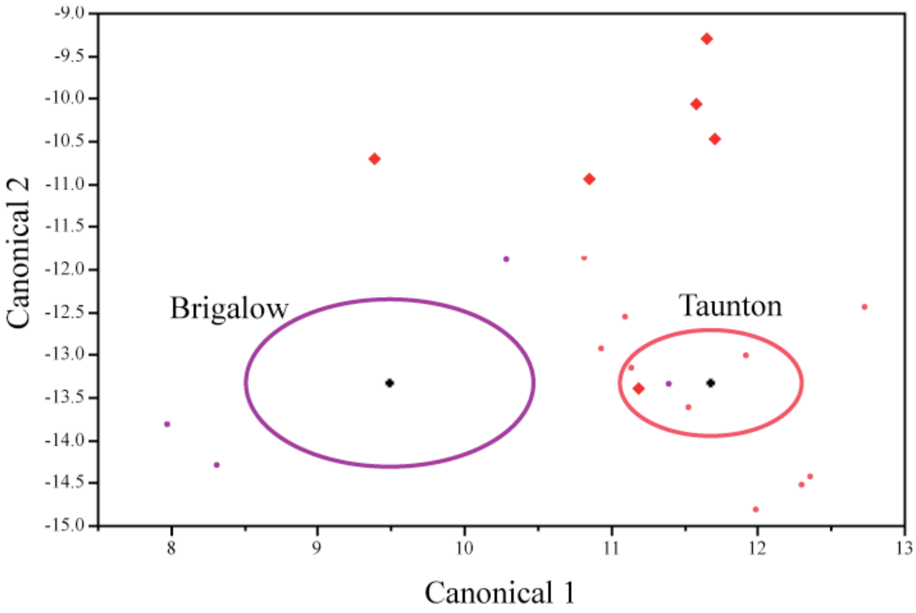
bower
other
competitor
aggressive/predatory

Figure 2(a) Repertoire size and composition of bowerbirds at Taunton both years combined; (b) Repertoire size and composition of bowerbirds at Idalia both years combined; (c) Repertoire size and composition of bowerbirds Brigalow both years combined.

Mimetic renditions of pied butcherbirds and whistling kites did not differ among field sites (butcherbird: Wilk's $\lambda = 0.47$, $F_{(1,13)} = 0.98$, $p = 0.52$; kite: Wilk's $\lambda = 0.007$, $F_{(2,11)} = 1.18$, $p = 0.55$). There was also low repeatability in the measurement that explained the most variation in mimicry among sites for butcherbird mimicry (proportion time to peak: r = 0.13) but renditions of kite mimicry were more repeatable (start frequency: r = 0.55).

(a)



(b)

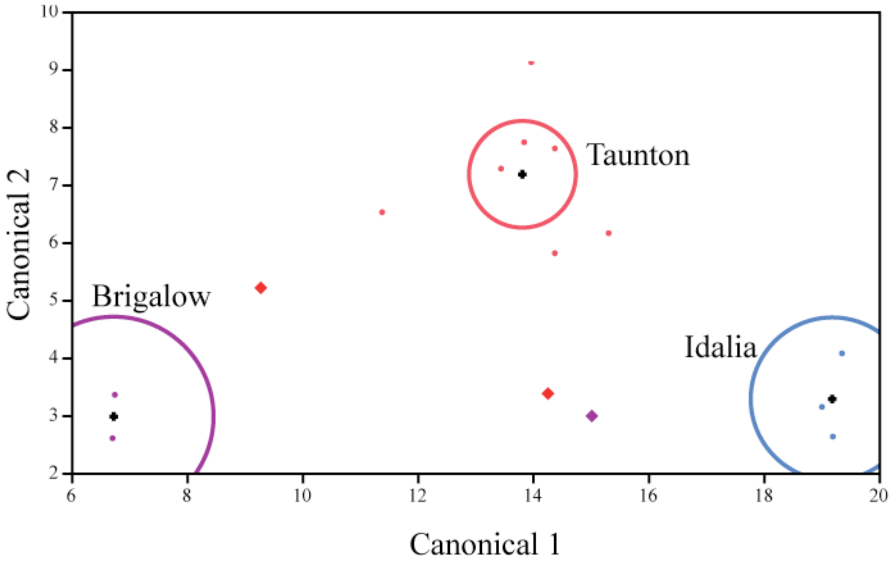
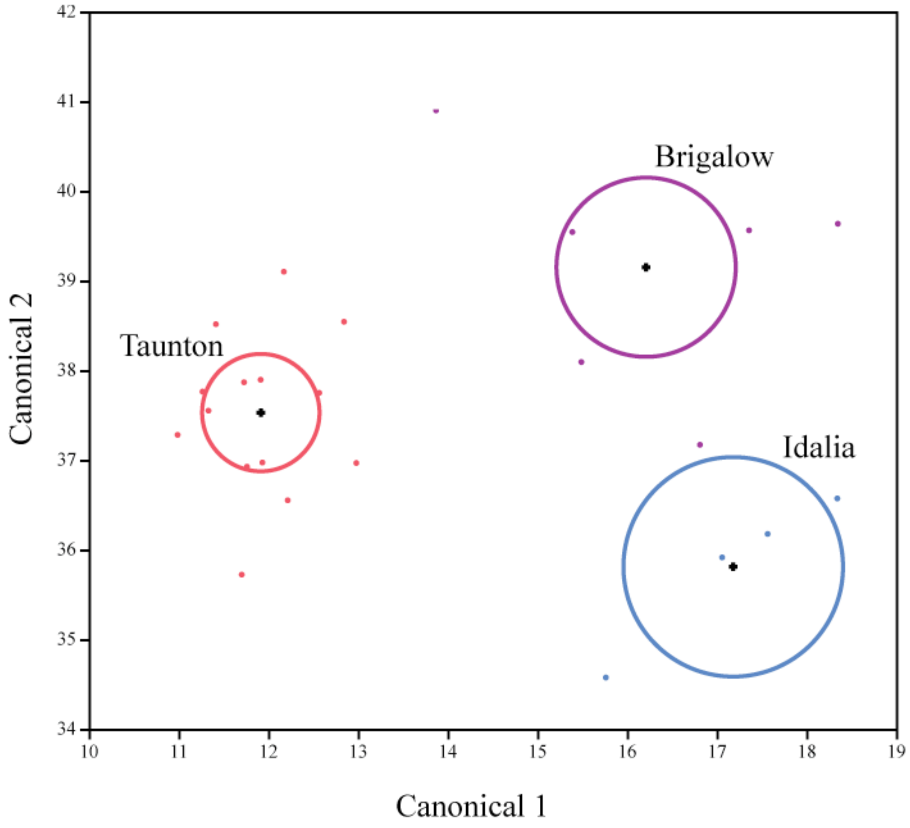


Figure 3(a) Discriminant function analysis of pied butcherbird mimicry at Taunton (red dots) and Brigalow (purple dots). Red diamonds present butcherbird model calls recorded at Taunton. Each dot represents the average of each individual bird's vocalisations, circles represent 95% confidence interval for each site's mean centroid value (black diamonds); (b) Discriminant function analysis of whistling kite mimicry at Taunton (red dots), Idalia (blue dots) and Brigalow (purple dots). Red diamonds represent recordings of model kites at Taunton and the purple diamond represent recordings of one kite at Brigalow.

Bowerbirds at each site produced structurally different renditions of 'advertisement' calls with high repeatability within sites (Wilk's $\lambda = 0.06$, $F_{(2,22)} = 10.43$, $p < 0.001$; maximum frequency $r = 0.89$; Figure 4a & b). Within sites, males at Taunton and Brigalow produced individually distinct 'advertisement' calls (Taunton: Wilk's $\lambda = 0.07$, $F_{(13,113)} = 4.82$, $p < 0.01$, $n = 14$; Brigalow: Wilk's $\lambda =$

0.32, $F_{(5,76)} = 4.96$, $p < 0.001$, n = 5) but individuals did not give very repeatable calls (Taunton: high frequency r = 0.37, Brigalow: low frequency r = 0.21). Males at Idalia did not produce individually distinctive 'advertisement' calls (Wilk's $\lambda = 0.55$, $F_{(3,39)} = 1.24$, $p = 0.25$, n = 4) and had low within-male repeatability (duration r = 0.15).

(a)



(b)

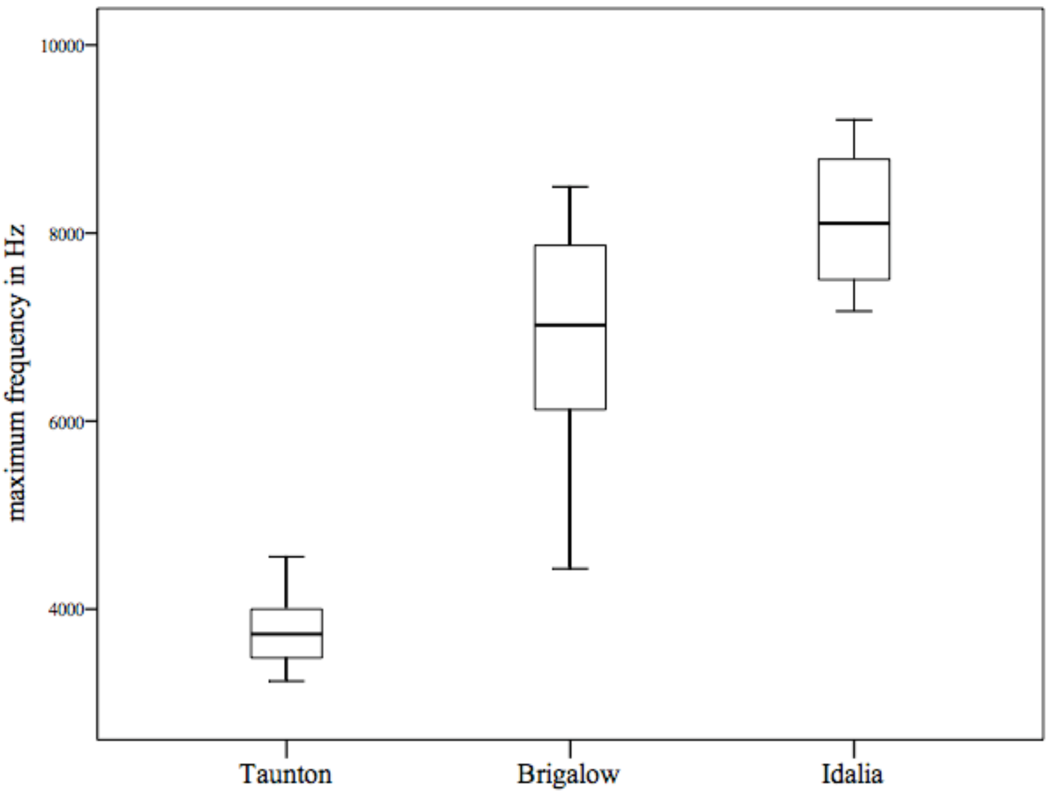
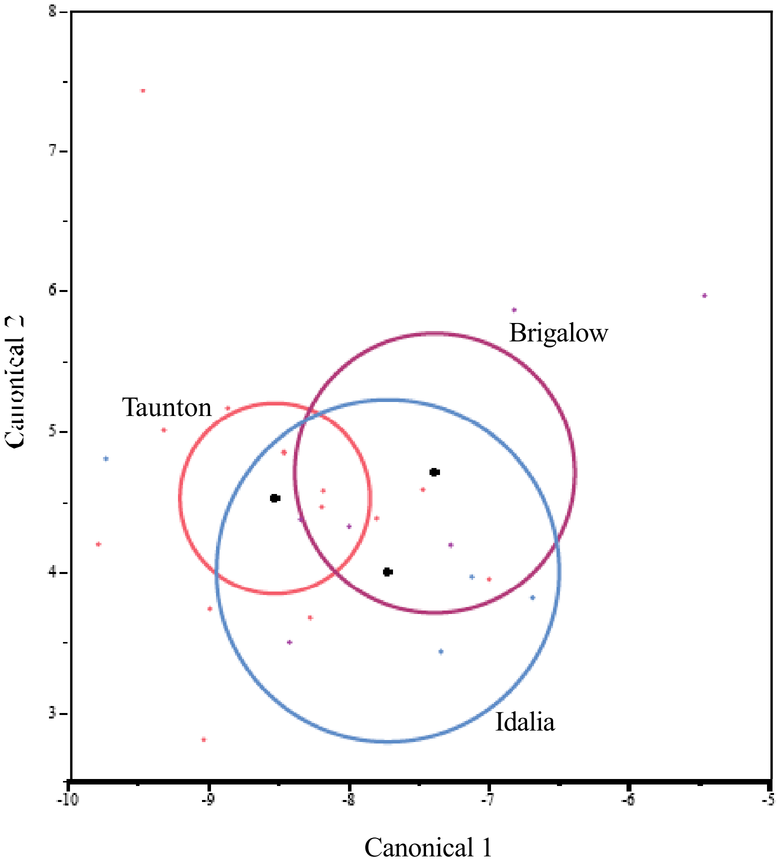


Figure 4(a) Discriminant function analysis of 'advertisement' calls at Taunton (red dots); Idalia (blue dots) and Brigalow (purple dots). Each dot represents one 'advertisement call' and circles represent the 95% confidence interval for the mean centroid value (black diamond) for each site; (b) Boxplot showing the difference in the variable (maximum frequency) that explained the most variance in 'advertisement' calls given at all three sites.

Males did not produce hisses that differed structurally among sites (Wilk's $\lambda = 0.72$, $F_{(2,21)} = 0.56$, $p = 0.83$, n = 14; maximum frequency r = 0.04; Figure 5a) although hisses were individually distinctive within sites (Taunton: Wilk's $\lambda = 0.21$,

$F_{(12,118)} = 6.08$, $p < 0.001$, n = 13, Figure 5b; Idalia: Wilk's $\lambda = 0.27$, $F_{(3,67)} = 8.98$, $p < 0.001$, n = 4; Brigalow: Wilk's $\lambda = 0.50$, $F_{(4,92)} = 4.68$, $p < 0.001$, n = 6). Individuals at Idalia and Taunton had higher hiss repeatability (Taunton: duration r = 0.54; Idalia: duration r = 0.56) than did individuals at Brigalow (maximum frequency r = 0.24).

(a)



(b)

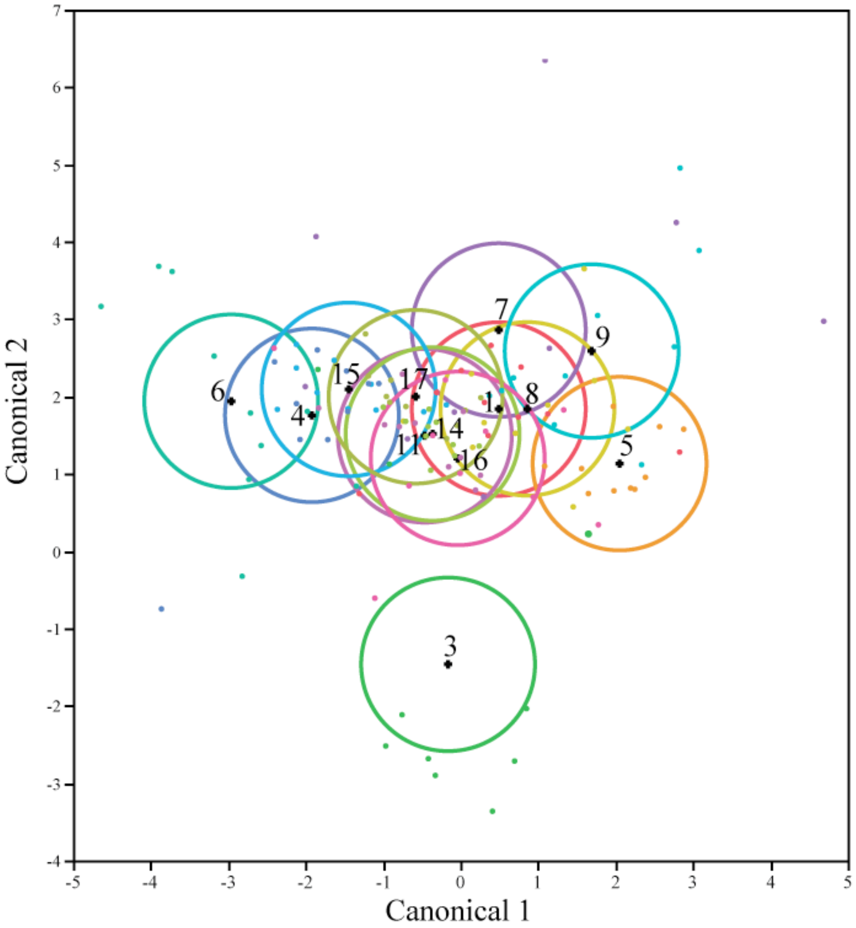


Figure 5(a). Discriminant function analysis of hisses given by bower-owning males at Taunton (red dots); Idalia (blue dots) and Brigalow (purple dots); (b) Discriminant analysis of individual bower owners at Taunton. Each dot represents one hiss and circles represent the 95% confidence interval for the mean centroid value (black diamond) for each individual.

Discussion

A significant proportion of species that were mimicked at Taunton were both present and mimicked at the other two geographically distant locations. Furthermore, it was the same vocalisation from each model species that was copied in all three locations. With one exception (crows), model species that were mimicked at one site only were observed only at that site. Crows were observed at all three sites but were only mimicked at Idalia. The mimicry of pied butcherbirds and of whistling kites was structurally similar at all three sites. The variation in the structure of the species-specific vocalisations varied depending on the vocalisation. Species-specific hisses did not differ structurally among sites although males within each site produced individually distinctive hisses. The structure of ‘advertisement’ calls, however, differed both among and within sites. Most of that variation was due to differences in the maximum frequency of calls.

The finding that bowerbirds mimicked approximately the same subset of species from different soundscapes could be interpreted in one of two ways: (1) males are selectively learning these specific sounds from the acoustic environment, or, (2) males are predisposed to learn these sounds due to some aspect of their acoustic properties. In Chapter 2 I showed that aggressive species were over-represented in the mimetic repertoire and suggested that mimicry may be used by the Taunton bowerbirds to deter predators or competitors. The vocalisations of aggressive and predatory species made up the majority mimetic repertoires at both Idalia and Brigalow, which supports my assertion that mimicry may be used deter heterospecifics. However, the sounds that were mimicked at Idalia and Brigalow also had the same structural properties as those mimicked at Taunton. As these sounds were all relatively simple and loud in the acoustic environment, I cannot exclude the hypothesis that these sounds are mimicked due to their simplicity and loudness.

Model selectivity has also been shown in geographically isolated populations of superb lyrebirds *Menura novaehollandiae*, where males at different sites mimic the same species (Zann and Dunstan 2008). It appears that these particular models may be mimicked as they contain sounds that are physically challenging to produce, such as a frequency sweep (Zollinger and Suthers 2004). Mature males mimicked these sounds more accurately than did immature males, which suggests that mimicry may act as an age-dependent signal. Evidence of this would require determining whether a more distant population of lyrebirds with a different suite of potential models mimicked sounds that were difficult to produce and that males improved in their mimetic accuracy of these sounds with age. Superb lyrebirds in the same age categories at both sites gave similar renditions of mimetic sounds. Although I do not know the ages of the male bowerbirds at the three sites (200 - 600 km apart), they gave similar renditions of butcherbird and kite mimicry. It seems unlikely that this was because they were all of comparable age.

I found that although males at different sites mimicked the same suite of models, mimicry of these models was not structurally different in contrast to our findings concerning the structure of mimicry at Taunton (Chapter 4). This could be due to two reasons: (1) mimicry only varies on a local scale as bowerbirds are copying the vocalisations of local birds, and this variation is not visible when comparing mimicry on a large scale; (2) I did not obtain enough recordings of mimicry from Idalia and Brigalow to distinguish the variation present in these vocalisations. More recordings of butcherbird and kite mimicry at these sites would be required to distinguish between these hypotheses.

By comparing mimetic vocalisations to the model species being mimicked, Zann et. al (2008) showed that although the model sound was similar between two sites, the mimicry was structurally distinct from these model sounds. Mimicry produced by Albert's lyrebirds *Menura alberti* at different sites is also structurally distinct from the model vocalisation being mimicked (Putland et al. 2006). Consistent with these findings, bowerbird mimicry was not an exact copy of butcherbird or kite model vocalisations. There may be several explanations for this: (1) males may be imperfectly copying models; (2) they may be accurately copying a signal that has degraded when it reaches them through the undergrowth; (3) males are modifying their mimicry to be more similar to mimicry produced by other males or (4) the use of discriminant function analysis to identify what structural measurements accounted for variation among sites may not access the appropriate structural variation in the sounds. I showed previously that males do not mimic very often in the presence of conspecifics (Chapter 3) and that males with closer bowers do not produce more similar mimicry when compared to more distant bower-owning males (Chapter 4), so males are unlikely to be modifying their mimicry to match conspecifics. It is possible that due to the low number of recordings of mimicry and models from all three sites that I have not captured the variation present in either set of sounds. Further recordings would be required to eliminate this possibility. If I have described the variation in both model and mimic sounds appropriately, it seems most likely that males are imperfectly copying models or copying degraded signals, similar to findings in Albert's lyrebirds (Putland et al. 2006).

Differentiating between imperfect copying and copying degraded signals might be achieved by determining whether the 'accuracy' of mimicry changes for different models being mimicked. If bowerbirds are imprecisely copying model vocalisations then I would expect them to be less accurate at copying certain aspects of sounds that seem to be difficult to imitate or learn (for example, high trill rate, frequency sweeps, abrupt changes in frequency; Zollinger and Suthers 2004; Ballentine 2009). If bowerbirds are accurately copying a degraded signal I would expect closer matching between model and mimicked sounds for models that vocalise in open spaces when compared to models that vocalise in vegetation. For example, I would expect that mimicry of a vocalisation that is produced when in open air (flying) might be more accurately copied than would the vocalisation produced by a species when in vegetation as there would be less opportunity for degradation of the sound travelling through open air. Comparing the sounds of models and mimics found in open and dense habitats would also help to determine whether sound degradation was an important source of variation in the structure of mimicry (Blumenrath and Dabelsteen 2004).

Despite the structure of mimetic vocalisations being similar at three sites, male bowerbirds produced structurally different ‘advertisement’ calls at each site. Geographic variation has also been observed in the more complex ‘advertisement’ calls of satin bowerbirds as males in similar habitats produced more similar ‘advertisement’ calls when compared to males in dissimilar habitats (Nicholls and Goldizen 2006). Calls appeared to be adapted for effective transmission in each habitat type, whereby males in denser habitats produced calls that had a lower frequencies and less frequency modulation compared to calls given by males in more open habitats (Hansen 1979; Nicholls et al. 2006; Boncoraglio and Saino 2007). Although not explicitly measured, Taunton had higher vegetation density than Idalia and Brigalow that may explain site variation in ‘advertisement’ calls. As I would predict from the findings outlined above, ‘advertisement’ calls produced by males at Taunton had lower frequency than those produced by males at Idalia or Brigalow. The among individual differences in these calls suggests that they may be used for individual identification. ‘Advertisement’ calls are thought to either attract potential mates to the bower or repel rival males, and it could be advantageous to possess an individually identifiable long-range vocalisation. For example, as female satin bowerbirds preferentially visit the bowers of males with whom they have previously mated (Uy et al. 2006) males may use ‘advertisement’ calls to remind a previous mate to the location of the bower site. If these calls are unique to individuals and used to identify males over long periods of time I might expect that they would be highly repeatable over long periods of time.

In contrast, the species-specific hiss did not vary structurally across the three sites. However, individual males within sites produced hisses that were structurally distinct from hisses produced by other males. Hisses may act on a local scale to mediate aggression or facilitate individual recognition. Monitoring the response of a bower-owning male to recordings of hisses from local and non-local bowerbirds could test this. Most aggressive interactions are between neighbouring bower-owning males (Madden et al. 2004) so I would expect vocalisations of neighbours to elicit a stronger response than would recordings from bowerbirds with more distant bowers. It would also be useful to determine whether female hisses are structurally distinct from male hisses and whether they are also unique to individuals.

These results suggest that the species-specific vocalisations of bowerbirds may be more complex than anticipated. Playback experiments would be useful to determine whether the geographic variation in the structure of these vocalisations is a result of social or ecological factors. It would also be useful to obtain more recordings of mimicry from Idalia and Brigalow to determine whether males within these sites give individually distinctive renditions of mimicry, as do males at Taunton. Here I have started to address the factors that may cause geographic variation in both mimetic and species-specific vocalisations.

CHAPTER SIX: IS MIMICRY AN INDICATOR OF MALE QUALITY?

I collected and analysed the data and wrote the first draft of this chapter, which was then completed in collaboration with S. D. Healy

Summary

Male bowerbirds use a multi-component display to attract females, and satin bowerbirds include vocal mimicry as part of this display. Although the closely related spotted bowerbird is unlikely to use mimicry in their sexual displays, mimicry may be an indicator of male quality in general. I determined whether mimetic repertoire size or rate of mimicry was correlated with any indicator of male quality in terms of predicted mating success. I also determined whether rate of species-specific hisses or ‘advertisement’ calling was related to male quality. Apart from one year where hiss rate when alone was negatively correlated with tenure, I found no evidence that any aspect of male vocalisation was correlated with any proxy for male quality. These results suggest that mimicry is not used in mate choice in spotted bowerbirds and that the rate of species-specific vocalisation is a poor indicator of male quality.

Introduction

Bowerbirds are well known for their elaborate constructions used in sexual display (Humphries and Ruxton 1999; Borgia 1995) but much less famous for their vocal skills. And yet, most bowerbirds are proficient mimics. One explanation for their mimicry is that they use it to enhance their sexual display either to attract females or to repel rival males (Coleman et al. 2007; Loffredo and Borgia 1986; Robson et al. 2005). To this end, either or both the size of the mimetic repertoire and the amount of mimicry produced may be used by a female or a rival as a proxy for male quality if the acquisition or production of mimicry is costly or age-dependent. In non-mimetic song, repertoire size may reflect age (Kiefer et al. 2006) or may reflect other aspects of male quality such as exposure to stress or parasite load (Nowicki et al. 2000; Buchanan et al. 1999). Furthermore, singing duration may reflect male quality (Oberweger and Goller 2001; Dolby et al. 2005; Buchanan et al. 2003).

Some birds use mimicry in a similar way to the way in which song is used: male satin bowerbirds *Ptilonorhynchus violaceus* with larger mimetic repertoires have higher mating success than do males with smaller repertoires (Coleman et al. 2007). The sounds that are mimicked may also reflect male age or quality: older superb lyrebird *Menura novaehollandiae* males copy the vocalisations of model species more accurately than do younger males and satin bowerbird males that produce accurate mimicry have higher mating success than rival males that produce less accurate mimicry of the same species (Zann and Dunstan 2008; Coleman et al. 2007).

Satin bowerbirds are the only members of the *Ptilonorynchus* genus that have been shown to use mimicry to attract a mate, despite mimicry being reported in all other members of the genus (Frith and Frith 2004). Four other members of this genus (spotted bowerbird *Ptilonorhynchus maculatus*, fawn-breasted bowerbird *Ptilonorhynchus cerviniventris*, western bowerbird *Ptilonorhynchus guttata* and great bowerbird *Ptilonorhynchus nuchalis*) are thought to use mimicry defensively as there are numerous anecdotal reports detailing mimicry of predatory species (Frith and Frith 2004). Consistent with this hypothesis, the mimetic repertoires of spotted bowerbirds *Ptilonorhynchus maculatus* are predominantly composed of aggressive species (Chapter 2 & 5; Coe 2005). However, these sounds may be mimicked not as a signal of aggression but instead as part of the sexual display. Satin bowerbirds mimic two of the same aggressive species as the spotted bowerbird, the laughing kookaburra *Dacelo novaeguineae* and Australian raven *Corvus coronoides* as part of their sexual display, so the origin of these sounds may not be useful for determining the function of such mimicry. If males were using mimicry in their sexual display I would expect mimetic rate to increase in the presence of conspecifics, but in Chapter 3 I found that this was not the case. However, mimicry may be an indicator of male quality in general, in which case I would predict that aspects of mimicry (such as rate of mimicry or repertoire size) would be correlated with male quality.

Male spotted bowerbirds construct bowers out of grass and sticks that they then decorate with predominantly green objects. These bowers are constructed afresh every mating season and are the site of male display to potential mates and male-male antagonism. When a female arrives at the bower area the male displays by vocalising, hopping round the bower, flapping his wings and tossing decorations (Frith and Frith 2004). Although males do not produce mimicry as part of these displays, mimicry may be correlated with other indicators of male quality so quantitative or qualitative measures of mimicry should be positively correlated with (indeed, lead to enhanced) male mating success.

I determined whether mimicry is an indicator of male quality in spotted bowerbird males by determining whether any aspect of mimicry (rate, repertoire size, accuracy) was correlated with male quality. I used associated indicators of male quality in bowerbirds rather than mating success, as the latter is often difficult to measure directly. In bowerbirds male quality is indicated by the number of certain decorations the male has on his bower and the quality of his bower construction, both of which are correlated with mating success (Madden 2003a, b; Borgia 1985).

I also determined whether species-specific vocalisations were indicators of male quality. Hiss rate increases in the presence of conspecifics (Chapter 3) and male satin bowerbirds that display at high rates (which include species-specific vocalisations) when alone at the bower are visited more often by females than are males displaying at a low rate (Robson et al. 2005). Thus I would expect that males with higher rates of vocalisation are of a higher quality than those males with lower vocalisations rates. Similarly, it is feasible that the long distance ‘advertisement’ call may be used by males to signal bower location to potential mates or to deter rival males. Satin bowerbirds females visit several bowers before choosing a mate (Uy et al. 2001) and the rate of ‘advertisement’ calling may allow them to identify high quality males from a distance. The advertisement call may be especially relevant in this context to the spotted bowerbirds as their bowers are typically at some distance from one another (at Taunton National Park for example, the typical inter-bower distance is >1km). It is feasible that males with higher quality bowers call at a higher rate than do younger males because they are better able to defend their bowers from marauding by rival males (Madden 2002).

Methods

I recorded the vocalisations of 19 male bower-owning spotted bowerbirds in Taunton National Park (23.3ºS, 149.1ºE), central Queensland, Australia, in July to November 2007 and 2008. Individuals were identified by a unique series of colour bands on both legs. Males were recorded vocalising at their bowers using a Sennheiser ME66/K6 microphone and power supply onto a Sony TCD-D8 DAT recorder at a sampling rate of 44.1kHz. All recordings were carried out by an observer sat approximately 10-15m from the bower and took place between 5:00am and 2:00pm. Recording sessions lasted between three and seven hours and the average time spent recording at each bower was 16 ± 0.95 hours (mean ± SE) per bower in 2007 and 17.13 ± 2 hours in 2008.

I identified mimicry by listening to recordings and visually inspecting spectrograms and I created repertoire profiles detailing the repertoire size and composition of each banded individual. Rate of mimicry of the bower owner was determined by calculating the duration of mimicry divided by the amount of time the bower owner was present. The rate of species-specific hisses and 'advertisement' calls were calculated in the same way.

The number of *Solanum* berries, which are green and common on spotted bowerbird bowers, is a good predictor of that bower owner's mating success (r = 0.49 to 0.65; Madden 2001). The number of *Solanum* berries was counted and bower quality assessed approximately every 36 days in 2007 and every 33 days in

2008: these measurements were taken four times in 2007 and three times in 2008. The quality of the bower construction was judged, using the same observer each time and a scale of one to four, using the following criteria (Figure 1; Madden 2001):

1. Avenue walls are present, but comprise only a grass or stick component that is incomplete;
2. Avenue walls are present and contain both grass and stick components, but both of these components are incomplete;
3. Avenue walls are present and contain both grass and stick components, but one of these components is incomplete;
4. Avenue walls are present and contain complete grass and stick components.

Figure 1. Two bowers maintained by males at Taunton. Left: a bower scored 4 for quality with complete grass and stick components. Note green *Solanum* berries in avenue; right: a bower scored 2 for quality as both components are present but incomplete.

The number of *Solanum* berries and bower quality scores were averaged for each bower owner for each year. I used bower tenure as a proxy for age. The duration of bower tenure is known for many individuals as this population of bowerbirds has been monitored intermittently since 1998 (1998, 1999, 2000, 2002, 2003, 2007, 2008). Bower tenure was estimated for males lost during unmonitored years using the known last year of tenure while for the individuals that became bower owners during unmonitored years I used the minimum known tenure.

Spearman's correlations were used to determine whether repertoire size or rate of mimicry was correlated with measures of male quality (number of *Solanum* berries, bower quality and tenure). Dunn-Sidak corrections were then applied. I also tested for relationships between species-specific vocalisations and measures of male quality.

Results

There were no correlations between any measures of male quality in either year (tenure, number of *Solanum* berries and bower quality: $r = -0.11$ to 0.37, $p = 0.15$ to 0.97) so I tested for correlations between all measures of male quality and mimicry. Neither the rate of mimicry nor repertoire size was correlated with any aspect of male quality in either year (2007: $n = 18$; 2008: $n = 13$; Table 1). The average duration between the occurrence of mimicry and the arrival of a conspecific in the bower area was 67.9 ± 12.8 minutes (mean ± SE).

Hiss rate when alone was strongly negatively correlated with tenure ($r = -0.69$, $p = 0.003$). No other aspect of hiss rate was correlated with any aspect of male quality in either year (2007: $n = 16$; 2008: $n = 13$; Table 2). Variation in 'advertisement' call rate was also not explained by any aspect of male quality in either year (2007: n = 17; 2008: n = 13; Table 3).

		2007		**2008**	
	Variable	**r**	***p***	**r**	***p***
Repertoire size	Tenure	-0.294	0.24	-0.13	0.66
	Number of *Solanum* berries	-0.55	0.02	0.34	0.26
	Bower quality	-0.24	0.34	-0.45	0.12
Rate of mimicry	Tenure	0.21	0.40	-0.07	0.83
	Number of *Solanum* berries	-0.47	0.85	0.22	0.48
	Bower quality	0.17	0.50	-0.23	0.45

Table 1. Spearman's correlations of two measures of mimicry (repertoire size and rate of mimicry) against measures of male quality in both years.

		2007		**2008**	
	Variable	**r**	***p***	**r**	***p***
Hiss alone	Tenure	-0.69	0.003	0.24	0.43
	Number of *Solanum* berries	0.85	0.75	-0.53	0.06
	Bower quality	-0.21	0.94	-0.37	0.22
Hiss with conspecific	Tenure	-0.05	0.86	-0.07	0.82
	Number of *Solanum* berries	-0.55	0.03	0.43	0.14
	Bower quality	-0.50	0.49	-0.11	0.73

Table 2. Spearman's correlations between aspects of male quality and hiss rate when alone or when with a conspecific in both years.

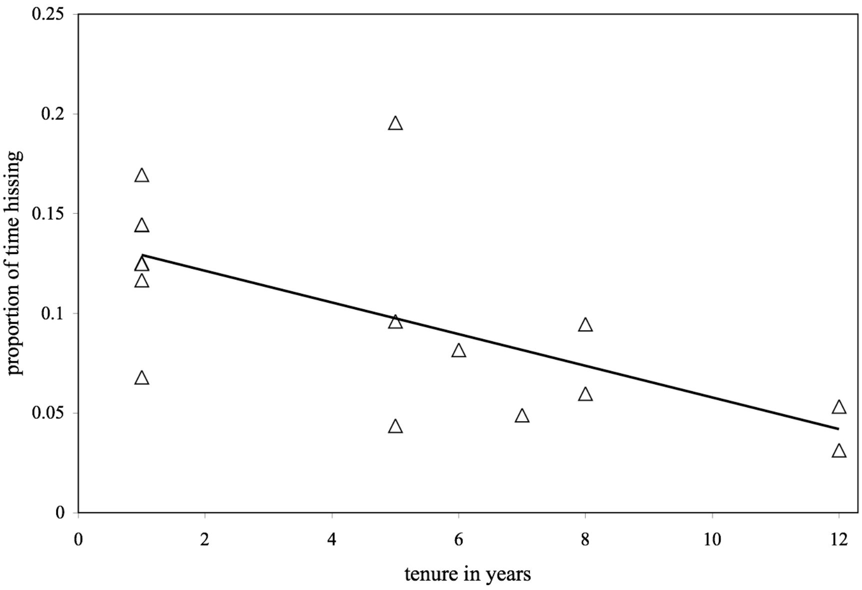


Figure 2. Correlation between tenure and average proportion of time hissing in 2007 (n = 16; $r^2 = 0.42$). Each triangle represents an individual bowerbird.

	2007		**2008**	
Variable	**r**	***p***	**r**	***p***
Tenure	-0.34	0.18	0.36	0.22
Number of *Solanum* berries	-0.54	0.84	-0.44	0.13
Bower quality	-0.16	0.55	0.10	0.76

Table 3. Spearman's correlations for aspects of male quality and rate of 'advertisement' calling in both years.

Discussion

There was no relationship between any vocalisations and measures of male quality apart from the finding that older males spent less time hissing in 2007. The aspects of mimicry that I measured do not appear to play a role in sexual selection in the spotted bowerbird, which is in apparent contrast with the reports that three other bowerbird species use mimicry when displaying to females (satin bowerbird *Ptilonorhynchus violaceus*, tooth-billed bowerbird *Scenopoeetes dentirostris* and regent bowerbird *Sericulus chrysocephalus*; Frith and Frith 2004). In satin bowerbirds, repertoire size is positively correlated with male mating success as well as with the number of decorations and the quality of the bower (Coleman et al. 2007). It appears that mimicry in this species may even be a more important component of the sexual signal than the bower itself: both the accuracy of mimicry and mimetic repertoire size explained significant amounts of variation in mating success whereas the number of decorations and bower quality were apparently unimportant when the sexual display as a whole was considered. I, however, found no relationship between mimicry and any of the proxies for male quality. It seems unlikely that these proxies are not useful predictors of male quality as they have been shown to be positively correlated with mating success (Madden 2001). However, the aspects of male display that are important in mating success also appear to be variable between years: in one year bower wall height, the number of citrus berries, the number of snail shells and the number of pieces of wire were all positively correlated with mating success ($r = 0.48$ to 0.59) but were not the following year (Madden 2001). In this study, I only used those indicators (number of *Solanum* berries and bower quality) that were strongly positively correlated with the number of matings in both years. These indicators are likely to be an honest signal of male quality that is policed by other males: when the number of *Solanum* berries present at bowers was artificially increased the number of bower destructions by rival males increased (Madden 2002). However, due to the multiple components of the sexual display in bowerbirds, it seems unlikely that male mating success can be described solely using these measurements. Other aspects of the decorations themselves, such as their colour, placement or contrast with the background may well be important

(Endler and Day 2006; Endler and Thery 1996), as well as the other aspects of the display such as paint, male colouration and male behaviour (Bravery et al. 2006; Doucet and Montgomerie 2003; Patricelli et al. 2003). It is also unclear how the number of matings a male obtains is related to his actual reproductive success. Female bowerbirds may mate with more than one male so the number of matings is not necessarily a good predictor of male reproductive success (Uy et al. 2001).

Although rate of hissing increased significantly in the presence of conspecifics there was no clear relationship between rate of species-specific vocalisations and male quality. Although older males tended to vocalise less in 2007 than did younger males, this was not the case in 2008. There are several plausible explanations for this between-year variation: (1) the sample sizes were small and thus the data were susceptible to Type I errors; (2) my measurements of male ‘quality’ are not representative of male mating success; (3) that neither of these were problems and that there really is variation between years in the way in which birds use their vocalisations. I know of few data that bear on this possibility although it is the case that females vary across years (and studies) in the attribute(s) they find attractive and it seems possible that males also may vary in the way in which they display their quality across years (Coleman et al. 2004; Madden 2001). Also, spotted bowerbirds are sexually monomorphic so I could not distinguish between vocalisation rate in the presence of males and vocalisation rate in the presence of females. It may be that the rate of vocalisations in the presence of females alone is an indicator of male quality, but to confirm this would require every female within a site to be identifiable as such (O'Loghlen and Rothstein 2010).

Overall, I found little evidence for a relationship between any aspect of male vocalisations and male quality. This outcome can be interpreted in several ways: (1) my proxies for male quality were a poor representation of actual male quality; (2) females base their choice of mate solely on visual displays; (3) females use acoustic cues other than rate of vocalisation to select mates; or (4) females assess males using a variety of the components that make up the male display, such that no single component is highly correlated with mating success. The first possibility I discussed above. With regard to the second, the importance of visual displays in spotted bowerbird mating success is well documented (e.g. Borgia 1995; Madden 2003b) and it seems entirely plausible that, in this bowerbird species at least, vocalisations play little role in displaying male quality.

A third possibility is that the measurements I used to quantify mimicry, hissing and 'advertisement' calls may have been inappropriate. For satin bowerbirds it appears that it is the accuracy of mimicry that is the important factor in male mating success. Although I did not measure the accuracy of mimicry here, the fact that mimetic rate does not increase in the presence of females (unlike in satin bowerbirds), suggests that mimicry is either not used in the sexual display of spotted bowerbirds or is used in some other way. Hiss rate did increase in the presence of conspecifics and may be used in sexual display. As hiss rate did not correlate with my proxies for male quality, I would need to determine whether hissing was correlated directly with male mating success to confirm its importance as a sexual signal.

Finally, for the closely related satin bowerbird there is evidence that each aspect of the male display provides females with different information, and these signals include mimicry, bower construction, number and type of decorations, painting behaviour, display intensity and display duration (Borgia 1985; Bravery and Goldizen 2007; Patricelli et al. 2003; Robson et al. 2005). It seems likely that one or more of these components of sexual display is also important in spotted bowerbird sexual displays, but it is feasible that mimicry is not one of these. It seems unlikely that mimicry produced by male spotted bowerbirds is used in sexual display, unlike its role in the closely related satin bowerbird.

CHAPTER SEVEN: GENERAL DISCUSSION

In the introduction I outlined the main hypotheses that may explain vocal mimicry in bowerbirds. I now revisit and discuss these hypotheses in the light of my work and focus on some of the broader questions arising from this. I also suggest directions for future research.

Interspecific communication

Mimicry may function to communicate with heterospecifics by deterring predators or competitors (Rechten 1978; Dobkin 1979). If this were the case, we would expect the vocalisations of predatory or competitor species to be mimicked and that mimicry would be produced in the presence of either predators or competitors. I found that bowerbirds preferentially mimicked the vocalisations of aggressive species and that these types of models were mimicked at three geographically isolated sites. These findings are consistent with mimicry acting to deter heterospecifics. However, naturally occurring heterospecific interactions with bowerbirds at the bower were very rare (three in two years), only involved one species (apostlebirds) and no mimicry was recorded during any of these interactions. Apostlebirds are not predators or competitors of bowerbirds so we would not expect them to elicit mimicry if it is used in a Batesian context.

Bowerbirds did, however, increase their rate of mimicry when a human was present at the bower. Humans may elicit mimicry for at least two reasons: (1) humans are a novel stimulus so bowerbirds react as to a predator; or (2) bowerbirds perceive humans as threatening and produce mimicry in response. If it is the novelty of humans that elicits mimicry then confirmation of this would require evidence that bowerbirds produce mimicry in response to any novel object presented at the bower and that the amount of mimicry decreases with repeated exposures. If humans are perceived as predators then presentation of other predators at the bower should also elicit mimicry. However, given that I never observed any heterospecifics apart from apostlebirds near the bower it is unclear why bowerbirds would need vocalisations solely to communicate in this situation. Mimicry was not a very common behaviour and it may be produced more often outside the mating season, when bower owners are not spending large amounts of time at their bowers and are therefore more susceptible to predation. Alternatively, if mimicry is used to deter competitors we would expect to bowerbirds to mimic when foraging rather than at the bowers where I made recordings.

Much stronger support for the use of mimicry as a deterrent would come from appropriate responses to playbacks of predators. If mimicry is directed at predators we would expect that playbacks of mimicry to predators would result in them being startled, confused as to the identity of their prey or deterred from attack in some other way (Rowe et al. 1986). If mimicry deters competitors from entering an area, then playbacks of mimicry at a known foraging site should result in heterospecifics moving away from that area. Lack of response to such playbacks, however, would not enable us to dismiss the deterrent possibility because it is not clear whether vocalisations from a predator are sufficient to invoke a response from a spotted bowerbird. It is also not clear whether a stationary visual stimulus can elicit a response. A previous experimental manipulation used to test the Batesian mimicry hypothesis (Coe 2005) presented bowerbirds with either a mount of a predatory species (brown falcon *Falco begoria*), an aggressive species (Torresian crow *Corvus orru*) or a non-threatening non-competitive species (spotted turtle-dove *Streptopelia chinensis*) in a tree near their bower. A control treatment was provided by the experimenter simulating the action of placing a mount in a tree. If mimicry was used in a true Batesian context we would predict that the bowerbirds would mimic in response to the mounts of the predatory or aggressive species. Mimicry was not produced in response to any of the mounts and there was a non-significant tendency for the control treatment to elicit a higher rate of mimicry than the other treatments. The feature of this control and human approaches to the bower is that movement was involved and this may be a crucial component of any stimulus that elicits mimicry. These findings are supported by a pilot experiment I carried out where a model snake was placed near the bower. The snake did not elicit any mimicry from the bower owner but when I walked to the bower to collect the snake the bower owner produced mimicry. It is therefore difficult to carry out appropriate experimental manipulations.

The behaviour of mimics when producing mimicry can be used to determine the function of mimicry. Spotted bowerbirds usually produced mimicry and species-specific hisses when on the ground or in bushes close to the bower. In contrast, ‘advertisement’ calls were produced by males perched in the top of trees within 20 metres of the bower. If spotted bowerbirds use mimicry in a Batesian context, we would expect them to be hidden when mimicking as the signaller is attempting to deceive the receiver as to their identity. Bowerbirds were not noticeably inconspicuous when they were mimicking but they may rely on their cryptic colouration to remain hidden, as they were often difficult to see when vocalising.

There is little evidence of Batesian mimicry in other species of mimics. Whilst burrowing owl mimicry of a rattlesnake rattle elicits alarm behaviour in ground squirrels, this sound appears to be a modified innate begging call rather than a learned vocalisation, and therefore not true mimicry (Owings et al. 2002). The mimicry of regent honeyeaters of other honeyeater species has been interpreted as Batesian mimicry (Veerman 1994, 1992). As is it honeyeaters that are being mimicked and these are not predatory this is more akin to mimicry of competitor species. As with great tits mimicking components of blue tit song, it is possible that when species are closely related with similar niches this kind of mimicry may be relatively common (Gorissen et al. 2006).

I found no evidence for mimicry being used to attract another species, either to assist during a predation event or to aid foraging efficiency. This may be because I didn’t observe these events. It also seems more likely, however, that use of mimicry in this way would be more appropriately used by species that live or forage in groups where both con- and heterospecifics pay attention to vocal signals (e.g. greater racket-tailed drongos; Goodale and Kotagama 2005), which spotted bowerbirds do not.

Intraspecific communication

Mimicry may function in sexual selection as an indicator of male age or quality or to communicate more generally with conspecifics. In the closely related satin bowerbirds, males incorporate mimicry into their sexual display and aspects of mimicry are correlated with male mating success (Coleman et al. 2007). In contrast, I found no link between any aspect of male mimicry and male display. Neither repertoire size nor rate of mimicry was correlated with any aspect of male quality and males did not increase their repertoire size between years. Whilst this could be due to a poor understanding of the various components that make up the male bowerbird display, mimetic rate was very low in the presence of conspecifics and did not attract conspecifics to the bower area. In spotted bowerbirds, mimicry seems unlikely to play a role in attracting a mate in this species. In satin bowerbirds and superb lyrebirds where mimicry does appear to play a role in sexual selection, it is not clear to which aspect of mimetic vocalisations females are paying attention. Accuracy appears to be relevant (Zann and Dunstan 2008; Coleman et al. 2007) but as in non-mimetic song, duration, within-song complexity, repertoire size and consistency may also be relevant (Botero et al. 2009; Leitao et al. 2006; Byers 2007; Holveck et al. 2008).

There is also little evidence that mimicry is used to repel rival males or to communicate with conspecifics more generally. If vocal mimicry was used to communicate with conspecifics in other ways, for example by allowing individual recognition or vocal matching to signal aggression, we would still expect the rate of mimicry to increase in the presence of other bowerbirds. The rate of mimicry did not increase in the presence of conspecifics and mimicry was very rare in this context. Thus it seems that mimicry is unlikely to be used to communicate with other bowerbirds.

Learning mistakes

Many of the data concerning mimicry in a wide range of species seem more consistent with the learning mistakes hypothesis than they do with other proposed hypotheses (Kelley et al. 2008; Garamszegi et al. 2007). This suggests that mimicry is a by-product of song learning ability, whereby sounds that are simple, common, loud and similar to the species-specific vocalisations may be learned in error. Learning mistakes is likely to be a good explanation for mimicry in many species where mimicry is only observed in isolated individuals, is produced rarely and where short motifs are copied. It is not difficult to see how such copying mistakes might arise in species that are open-ended learners with long, complex songs. However, it seems an unsatisfactory explanation for those species like spotted bowerbirds where the majority of individuals produce mimicry and where a multiple sounds are mimicked.

Spotted bowerbirds demonstrate some selectivity in model choice: they preferentially mimicked aggressive species at three geographically isolated sites. However, it is also the case that many of the sounds that were mimicked shared the same acoustic properties and were relatively simple. It feasible that these sounds are learned due to their simplicity and similarity to the species-specific hiss. It is unclear whether bowerbirds learn any aspect of their species-specific vocalisation but if they are not learned we may not expect males to ‘accidentally’ to acquire sounds that were similar to their species-specific vocalisations, as would be predicted by the learning mistakes hypothesis.

Although they are passerines, bowerbirds do not ‘sing’ in the typical sense and may therefore not learn any of their species-specific vocalisations. At least one model for song learning requires the use of a neural template to which a bird learning a sound matches what it hears with that template (Bolhuis and Gahr 2006). If there is no neural template or a broad neural template against which to compare an acquired sound then the vocalisations of heterospecifics may be acquired. This leads to the intriguing possibility that mimetic sounds may be acquired due to the absence of a neural template for learning sounds purely because species-specific vocalisations are not learned. One way to determine how sounds are acquired in mimetic species would be to look at the simplicity of the species-specific repertoire and the prevalence of mimicry. Several of the most famous mimics such as bowerbirds, lyrebirds and parrots have simple species-specific vocalisations, which suggests that species with simple species-specific vocalisations are more amenable to learning mimicry (Bell 1976; Pepperberg 1994).

There is some evidence that pure tone sounds and sounds with complex frequency modulation are difficult to produce (Suthers and Zollinger 2004; Zollinger and Suthers 2004; Podos 2001) so bowerbirds may be copying sounds that are relatively simple to replicate. However, several relatively complex sounds (for example, the whistling kite call) were also mimicked. An alternative explanation is that sounds that are learned are attention-grabbing or loud, which may explain why the vocalisations of predators and alarm calls appear to be mimicked more frequently than are other calls. It is difficult, however, to quantify loudness or salience as these measurements are somewhat subjective and difficult to quantify in the field. This issue may be more readily addressed in the laboratory, although it is unlikely that such experiments will be feasible on bowerbirds.

In summary, although my data are most consistent with mimicry functioning in a Batesian context, I cannot exclude the possibility that these sounds are mimicked as a result of their structural properties. However, if they are mimicked as a consequence of their structure, this does not explain why the rate of mimicry increases when males are disturbed at the bower by humans.

Learning

Although mimicry is generally assumed to be learned directly from the species being mimicked, it is also possible that mimicry may be learned from conspecifics (Putland et al. 2006; Hausberger et al. 1991). By surveying the mimetic repertoires of bower owners in Taunton, I found that males with bowers closer together shared more of the sounds in their repertoires than did males with bowers that were further apart. Whilst these results are consistent with mimicry passing from bowerbird to bowerbird, they could also be a result of bower owners copying the sounds in their local environment. By analysing the structure of two commonly mimicked models, I showed that structural similarity of mimetic sounds was not related to the distance between bowers, and therefore males were unlikely to be learning mimicry from each other. It would be useful to quantify how accurately male bowerbirds learn mimicry from models and to determine whether males learn from one model or whether they modify their mimicry with experience. At least two individuals learned a novel vocalisation from one model within a year of that vocalisation occurring in the acoustic environment, which confirms that bowerbirds can acquire sounds directly from the model that is being copied. For this vocalisation to enter into the mimetic repertoire it must have been learned by at least one bird directly from the model. This is also evidence that bowerbirds are open-ended learners as at least one of the birds that produced ‘Bonnie’ was at least five years old, and bowerbirds modified the contents their mimetic repertoires over time. That bowerbirds produced different mimicked sounds across the years does not confirm that they learned these sounds each year.

It is not clear how, when or why a mimic learns a new sound. For example, we do not know if sounds may be learned after just one exposure or if repeated exposure is necessary, or whether sounds are more accurately copied with practice or whether they remain structurally stable over time. These kinds of questions would probably be best answered using mimics in a laboratory setting, where it is possible to control the sounds to which birds are exposed and to record all vocalisations that are produced.

Species-specific vocalisations

I used the species-specific hiss as a ‘control’ to allow for useful comparisons between mimetic and non-mimetic sounds. I found that the species-specific hiss, unlike mimicry, increased in rate in the presence of conspecifics, which suggests that they serve different functions. This vocalisation is most likely to be used in conspecific interactions. Hisses appear to mediate interactions between bowerbirds whereas ‘advertisement’ calls function to attract females and/or repel rival males from the bower area. Both hisses and ‘advertisement’ calls demonstrated geographic variation in their structure although it is unclear whether this variation is a result of social or ecological factors. It is also not clear what information these sounds are conveying to conspecifics. I found no relationship between the rate of species-specific vocalisations and any aspect of male quality. However, as bowerbirds are sexually monomorphic I could not distinguish between hisses directed at males and hisses directed at females, which is likely to be an important distinction (O'Loghlen and Rothstein 2010). Other aspects of hissing apart from rate may also be relevant: in a previous study on spotted bowerbirds the proportion of long hisses to short hisses during male display was correlated with male mating success (Borgia and Presgraves 1998).

General conclusions

I have shown that attempts to capture the full repertoire of a mimic and to determine what contexts that mimicry is produced in can be useful in determining the function of mimicry in a particular species. Determining both the content and the context of mimicry would be a useful approach to take with species where we suspect we know the function, as often only one of these is quantified. Spotted bowerbirds are a useful study species in which to investigate the function of mimicry. Males were easy to locate and record during the mating season and I could easily measure male quality via their bowers. It was also relatively simple to identify mimetic vocalisations due to their small and distinctive species-specific repertoire. However, for future research it would be advantageous to study a species that was sexually dimorphic, where age could be easily determined and that mimicked regularly. Lyrebirds potentially fulfil more of the desired features for a useful system as they meet these criteria.

An important aspect of research on vocal mimicry concerns the objective identification of mimetic sounds. I was very conservative when identifying sounds as mimicry, and most likely discounted inaccurate renditions of mimicry. An automated procedure such as spectrographic cross correlation could be a useful way to standardise how mimetic sounds are identified, for example by accepting similarity values above a predetermined level. I quantified the structure of mimetic sounds by measuring spectrograms rather than using automated methods (Hamao and Eda-Fujiwara 2004; Khanna et al. 1997). Whilst automated methods such as spectrographic cross correlation can be useful, they are not sensitive to any shifts in frequency, which may be important given that mimics have been shown to substitute vocalisations of a lower frequency where the model sound is outside of their frequency range (Zollinger and Suthers 2004). This type of analysis also cannot be used to analyse broadband ‘noisy’ sounds, which were commonly mimicked by bowerbirds. When comparing two or more mimetic sounds it is important to consider the origin of the model call, given that many birds demonstrate individual and geographic variation in vocalisations. Using spectrographic measurements and then averaging these across individual models is a useful way to obtain a representative sound.

One of the more challenging questions to be addressed is the learning of mimicry, which is less accessible than learning of normal song because we know so little about what sounds are learned and when. Directing attempts to the window in which imprinting occurs might be a first step and brood parasites may provide a useful study system. Mockingbirds would appear to be a viable laboratory system as adults are amenable to learning heterospecific vocalisations from taped tutors. They also learn computer tones, which would allow a variety of features to be manipulated. This system could be used to investigate how many exposures to a sound a mimic requires before reproducing it, how accurate mimetic renditions are and how these change over time. A range of sounds that vary in amplitude, frequency and presence/absence of harmonics could also be presented to further our understanding selectivity of models in a captive environment. We should also be aware that the acquisition and reproduction of mimicry in captive species is likely to differ from those in wild mimics due to different acoustic and social environments.

Conclusions

Vocal mimicry in spotted bowerbirds is likely to serve an interspecific role by acting to deter predators or competitors and seems unlikely to function in any aspect of intraspecific communication. Mimicked sounds are learned directly from model species in the local habitat, which can lead to local patterns in repertoire sharing. Whilst these findings go some way towards addressing our lack of knowledge concerning vocal mimicry, experimental manipulations confirming that mimicry does indeed function in a Batesian context are required. Although experimental manipulations are maybe desirable, in this situation they were both impractical and based on Coe (2005), possibly unlikely to work. By recording both whole repertoires and analysing the structure of both model and mimic vocalisations it has been possible to make significant headway in understanding vocal mimicry.

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APPENDIX:

VOCAL MIMICRY IN SONGBIRDS

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ABSTRACT

In 1982, Baylis decried the serious lack of experimental verification for the various hypotheses proposed to explain vocal mimicry in songbirds. With few exceptions, our understanding of the function and acquisition of this fascinating behaviour seems to have scarcely progressed. I examine the proposed functional explanations and supporting evidence, and summarise advances made since Baylis' review. I conclude that there is no compelling evidence to support any of the functional hypotheses but, rather, that almost all of the data concerning song mimicry are consistent with the Learning Mistakes Hypothesis, whereby birds learn simple and common sounds, frequently using them in inappropriate contexts. Additionally, many apparently mimicked sounds are calls, not songs, which themselves may not be learned by the models. It is plausible that many examples of call mimicry are, in fact, due to evolutionary convergence.

Keywords: vocal mimicry, vocalisations, learning, song, call convergence, songbird

Vocal learning may be broadly split into two categories: copying of conspecifics and copying of heterospecifics or other sounds. In this review we focus on vocal mimicry, the copying of the vocalisations of another species or an environmental sound, specifically in songbirds, the most widely documented group. Twenty-six years ago, Baylis (1982) wrote an extensive review of vocal mimicry in songbirds, outlining possible functional explanations. It seemed likely then that there might be more than one such explanation for the existence of vocal mimicry but there were too few appropriate data to be sure. The purpose of this review is to revisit those functional explanations in light of the data that have been produced since 1982.

Functional explanations for vocal mimicry are inherently attractive given the complexity and accuracy of some of the mimicry. Additionally, there are many anecdotes in which birds are described as having used mimicry in a seemingly appropriate context. For example, egg collectors at nests of great bowerbirds *Chlamydera nuchalis* have reported hearing mimicry of cats, dogs and whistling kites (*Haliastur sphenurus*, a local raptor species) and this has been interpreted as an attempt by the nesting female to intimidate the approaching human (Frith and Frith 2004). However, as we will show, such interpretations do not explain the mimicry of other sounds and their use in other contexts by great bowerbirds or almost all other songbird mimicry.

Throughout this review we focus entirely on data published subsequent to Baylis' review, as in that review no consensus as to the importance of one functional explanation over another was reached. These data are fewer in the number of species than the data in a recent comparative review by Garamszegi (2007) but geographically more widespread, and the detail allows us to examine mimetic structure and the context in which mimicry is used.

I think it helpful to distinguish between calls and songs, although the distinction is somewhat arbitrary and there is no universal definition in the literature (Spector 1994). Here, we define calls as being simple, short, and produced by both males and females throughout the year in particular contexts, e.g. alarm, threat and so on (Catchpole and Slater 1995). Importantly, it is usually considered that they are not learned (although see Vicario et al. 2002) and that a brain pathway (with nuclei located in the midbrain) different from that involved in song is utilised in their production (Seller 1981). I define songs as, typically, long, complex, and largely produced by males for reproductive and territorial purposes (Marler 2004). They are usually learned either in early juvenile development or, in some cases, acquired throughout the bird's lifetime and a complex of brain nuclei in the forebrain is involved in learning and production.

Another distinction we would like to make is that between mimicry via learning and mimicry due to convergence over generations, as the processes involved in sound acquisition are entirely different. True vocal mimicry is typically considered to be the acquisition of sounds within an individual's lifetime, and, as such, must be learned. The learning mechanisms involved in mimicry are not focus of this review, although they may show significant similarities to those seen in song learning (Beecher and Brenowitz 2005). In contrast to true vocal mimicry, there is another process by which birds arrive at sounds that are very like the vocalisations of heterospecifics. Evolutionary convergence is likely to be seen between closely related species or result from the occurrence of similar selection pressures, where a common form of vocalisation is favoured. This process is the result of the genetic effects of selection accumulating over time and one in which learning plays no part. There is a third instance of mimicry, often termed vocal convergence or vocal matching, in which an individual changes its vocalisation to match those of another (see below). This type of matching is usually a response to conspecifics rather than to heterospecifics and is not the convergence we describe above (Gahr 2000). As such, we have not included instances of vocal matching among conspecifics in this review.

FUNCTIONS OF HETEROSPECIFIC VOCAL MIMICRY

A number of possible functional explanations for vocal mimicry have been suggested, which fall into two major categories: (1) Interspecific communication, for avoidance of threats and/or competitors; (2) Intraspecific communication, either in a sexual context or for social affiliation. Two common assumptions in all of these hypotheses are that mimicry is a separate category of sounds from calls and songs, and it is used in preference over other sounds in specific contexts.

INTERSPECIFIC COMMUNICATION

The Beau Geste hypothesis

By singing many different types of (species-specific) song, an individual may give a false impression that many individuals inhabit a territory and so deter potential intruders. Krebs (1977) originally proposed this Beau Geste hypothesis to explain the occurrence of large, species-specific song repertoires and Rechten (1978) suggested that it may apply to vocal mimicry, particularly for territorial birds. By mimicking the vocalisations of a wide range of heterospecifics, birds may reduce the chance that competitors for food or other resources enter their territory, especially if these potential intruders are themselves highly territorial and thus pay close attention to vocal signals.

In the 1970’s there was anecdotal evidence that some species incorporate heterospecific mimicry into their territorial advertisements, perhaps acting to deter heterospecific competitors (Curio 1978). Not only has there been no subsequent support for the hypothesis in the context of species-specific vocalisations (Yasukawa 1981; Dawson and Jenkins 1983; Haftorn 1995), it is also unclear why heterospecific song would be more effective at deterring potential competitors than conspecific song, unless competitors pay attention to the number of different species heard in an area. Without evidence to support this hypothesis in either in a species-specific or mimetic context, this seems an unlikely explanation for the occurrence of mimicry (MacDougall-Shackleton 1998).

The Beau Geste hypothesis also does not explain the occurrence of species (usually closely related) including sounds like those of heterospecifics in their own songs, seemingly so as to reduce aggression over territory boundaries (Baptista and Catchpole 1989). For example, great tits (*Parus major*) may include blue tit (*P. caeruleus*) songs (which sound significantly different) in their own vocalisations (Gorissen et al. 2006). There are at least two possible explanations for this kind of mimicry: firstly, due to competition for resources, mimicry has arisen so as to lower interspecific aggression, an idea that is similar to vocal matching of group members seen in parrots (Wright et al. 2005). Alternatively, it could be that great tits, because they interact so frequently with blue tits, mistakenly learn blue tit song. Discrimination between these two would be possible if the use of heterospecific mimicry leads to a reduction in aggressive interactions with those heterospecifics. Other instances seem best explained by copying of an inappropriate tutor as occurs when individuals are isolated or when allopatric species occasionally overlap (Helb et al. 1985).

Batesian acoustic mimicry

Dobkin (1979) suggested that mimics may deter competitors or potential predators by copying the vocalisations of animals that are predatory or agonistic, in a manner akin to that of a palatable species attempting to avoid predation by visually resembling a noxious species (Bates 1862). Competitor species may perceive a threat from an apparent predator, avoid entering the territory of the mimic, and thus not compete for resources. The intended audience may also include potential predators that are deterred from attacking the mimic by the threat of encountering another predator (Vernon 1973; Dobkin 1979), or are perhaps confused as to the identity of their proposed prey by the conflicting acoustic signals coming from the mimic (Harcus 1977; Curio 1978). I consider that the identification of mimicry of predators with Batesian mimicry in the colouration pattern context has caused some unnecessary confusion in that visual mimicry comes about through evolutionary convergence and not learning. Nonetheless, the predictions are that vocal mimics should learn predator vocalisations and then use those sounds in response to the presence of a predator or a competitor.

There have been no compelling experimental data collected that support or refute this hypothesis in the past twenty-six years. One possible example comes from the Australian magpie *Gymnorhina tibicen*, which mimics potential nest predators, the barking owl *Ninox connivens* and the boobook owl *N. novaseelandiae* (Kaplan 1999). However, not only are there no data on the context in which these sounds are used, but, given the diversity of sounds that magpies mimic, it would seem that Batesian mimicry is not the most parsimonious explanation for the mimicry of these two owls. Australian magpies can have a considerable mimetic repertoire, a very small proportion of which is mimicry of predatory species (other mimicry includes rosellas *Platcercus* spp, lapwings *Vanellus* spp, lyrebirds *Menura* spp). Call convergence in this species might be ruled out if there is considerable between-individual variation in repertoire content. However, if they learn these sounds from conspecifics (not yet known) they would be not considered to be true vocal mimics (copying from heterospecifics or the environment).

Another Australian species that mimics aggressive or predatory species is the spotted bowerbird *Chlamydera maculata* (Coe 2005). However, as mimicry is commonly produced in bouts along with non-predatory models such as grey-crowned babblers *Pomatostomus temporalis* and yellow-throated miners *Manorina flavigula*, it seems unlikely that the mimicry would be an effective deterrent for potential predators. Additionally, although one might expect this kind of deterrent to be effective only when the mimic is hidden from view, spotted bowerbirds frequently vocalise (including mimicry of predators) from conspicuous perches.

Experimental manipulations demonstrating that signallers give mimetic calls of predators or agonistic species when their territory, nest or safety is threatened, and that receivers respond to mimicry as if to vocalisations by a genuine predator would provide compelling evidence that mimicry is used as an acoustic aposematic signal (i.e. appropriate response to a specific context). In an apparent experimental test of the Batesian mimicry hypothesis, burrowing owl *Athene cunicularia* hisses (claimed to be mimicry of rattlesnake rattles) were played to ground squirrels, eliciting more avoidance behaviour from ground squirrels sympatric with rattlesnakes than from rattlesnake-naïve ground squirrels (Rowe et al. 1986). Playback of rattlesnake noise elicited a stronger response from the ground squirrels than did the owl hiss, but it is not clear whether the owls naturally use this hiss in a defensive response to rattlesnakes, a potential nest predator, or whether it functions to deter ground squirrels from competing for nest burrows. Importantly, this is not vocal mimicry as the hisses are not learned, rather, it appears that the hisses are a modified juvenile begging call and are the result of call convergence (Owings et al. 2002).

In our view, then, while there is a possibility the Batesian mimicry hypothesis may explain some of the components of the mimetic repertoire of some species, for most species' mimicry this is an implausible hypothesis. It is also clear how very few quantitative data exist that document the natural context in which mimicry is used.

Attracting a third species

Mimics might benefit by inducing mobbing of their own predators or competitors by individuals of one or more other species. Alternatively, alarm calls, including apparently mimetic ones, may attract a second predator, possibly coming in search of injured prey, giving the caller a chance to escape during the ensuing contest with the first predator (Hogstedt 1983; Curio 1978). While this might explain the use by phainopeplas *Phainopepla nitens* of mimicry of heterospecific alarm calls when distressed (e.g. when captured in mist nets) as it can elicit mobbing by heterospecifics, it does not fit with the stronger mobbing response evoked by playback of the phainopepla's own alarm calls (Chu 2001a, b). At the very least, this seems an inefficient use of mimicry. Eastern towhees (*Pipilo erthrophthalmus*) will also substitute their own alarm calls with mimicry of heterospecific alarm calls when disturbed. It is not yet clear what benefit is gained by doing this as behavioural responses of heterospecifics and conspecifics were not investigated (Greenlaw et al. 1998).

Greater racket-tailed drongos *Dircurus paradiseus* insert calls thought to be mimicry of alarm calls of heterospecific flockmates alongside their own mobbing calls (Goodale and Kotagama 2006a). They also use apparently heterospecific alarm calls in alarm situations, but this is done only as they increase the number of their own alarm notes and not all of the calls used are alarm calls. As phainopeplas also include non-alarm calls in stressful situations alongside alarm calls, it is possible that this less-than-perfect matching of context to the use of specific mimicry is due to a lack of our understanding of the context. However, there is no evidence that the drongos preferentially use heterospecific calls in alarm situations. There is also no evidence, yet, that they learn these calls in spite of these calls being labelled as heterospecific mimicry. Unusually, however, drongos do mimic songs of heterospecifics although these are relatively uncommon and are used inappropriately, i.e. in the same contexts as the alarm calls.

As drongos' feeding efficiency is higher when they forage within a flock (comprising con- and heterospecifics) than when foraging alone, it has been proposed that these birds utilise non-alarm mimetic sounds to attract other birds to form flocks. Indeed, playbacks of drongo non-alarm mimicry were more likely to attract other birds than were playbacks without mimicry although, intriguingly, the species attracted tended not be those species being mimicked (Goodale and Kotagama 2006b). Until there are substantive data on the context in which drongos themselves produce non-alarm calls, these playback data, while consistent with the attraction of a third species hypothesis, do not demonstrate that the drongos use mimicry in a context-specific way, i.e. only using mimicry appropriate to a specific situation.

Facilitating brood parasitism

Brood parasites face discrimination by their hosts and are commonly rejected at the egg stage, driving the evolution of visually mimetic eggs (Davies 2000). Hosts may also discriminate against brood parasite nestlings, perhaps noting the differences in begging calls that they give. To counter this, brood parasite nestlings may have been selected to produce begging calls very like those of their host young. For example, nestling Horsfield's bronze-cuckoos *Chrysococcyx basalis* may be accepted by superb fairy-wrens *Malurus cyaneus*, which reject shining bronze-cuckoo chicks, *C. lucidus*. Horsfield's bronze-cuckoo chicks have a similar begging call to that of the superb fairy wren chicks, both of which differ from the begging call of shining bronze-cuckoo chicks. The chicks of this latter species have a begging call very like that of the chicks of their usual host, the thornbill *Acanthiza* spp (Langmore et al. 2003). This may be mimicry by direct copying, especially if the parasite is raised alongside host young, so gaining an opportunity for learning the host chicks' begging calls (Redondo and Dereyna 1988). However, as this similarity in vocalisation has also been described for cuckoo species that eject the host's young and are raised alone, it is likely that this is not vocal mimicry but call convergence (McLean and Waas 1987; Madden and Davies 2006).

Vocal mimicry has been demonstrated in another brood parasite, the village indigobird *Vidua chalybeata*, which parasitises and mimics the songs of the red-billed firefinch *Lagonosticta senegala*. Female indigobirds mate with males that mimic the song of their host species. When indigobirds were experimentally foster-reared by Bengalese finches *Lonchura striata* they developed songs similar to their new foster parents, despite being able to hear and see firefinches, their usual host (Payne et al. 1998). Irrespective of host species, indigobird males did not copy songs directly from their host parents (unless isolated with them after fledging) but of other adults of the foster species or other indigobirds mimicking the same foster species. Learning host songs may occur in two stages: early life when the general features of host song are learned from parents, and a later developmental period when songs are learned from non-parents. This example does appear to be one of learning and the implication is that these mimicked songs are used to attract conspecific females.

In summary, with the exception of some brood parasites, none of the functional explanations for mimicry in an interspecific context has yet been strongly supported. In all cases, it appears that the birds either do not produce mimicry relevant to the appropriate context or, if they do, they are not very good at doing so. There is also no compelling evidence to suggest that the models mimicked are specifically chosen for later use in a particular context. Finally, there is almost no evidence for learning of vocalisations in any of these studies and thus no support for vocal mimicry itself.

INTRASPECIFIC COMMUNICATION

Sexual selection

A wide variety of models mimicked might be explained by sexual selection as mimetic vocalisations could provide an honest indicator of male quality (Zahavi 1975), with only the best males being able to learn and give accurate renditions of mimicry (Loffredo and Borgia 1986; Nowicki et al. 2002). Alternatively, females might demonstrate a preference for novelty, which could be achieved by a male by incorporating heterospecific song into his display (ten Cate and Bateson 1988). However, if females were only interested in repertoire size we would expect high levels of improvisation or invention.

The occurrence of mimetic sounds in the courtship displays of several bowerbird species is consistent with mimicry playing a role in mate choice. For example, a satin bowerbird *Ptilonorhynchus violaceus* male may include mimicry of up to five sympatric bird species alongside species-specific vocalisations in his courtship display. While older males tended to produce longer and higher quality bouts (of mimicry of laughing kookaburra *Dacelo novaeguineae* calls, spectrograms assessed by eye) than did younger males, in only one of two years in which mimicry was quantified did mimicry duration and quality result in higher mating success (Loffredo and Borgia 1986). More recently, and using a more sophisticated method of assessing accuracy of mimicry (spectrographic cross correlation), male satin bowerbird mimetic accuracy of both kookaburra and Lewin's honeyeater (*Meliphaga* *lewinii*) calls was positively correlated with mating success and accuracy was correlated positively with repertoire size (Coleman et al. 2007). However, these satin bowerbirds mimicked only five species, two of which featured only rarely in the vocal displays, suggesting that much potential for expanding repertoire was not being used. The possibility that satin bowerbird females prefer sounds that are physically difficult for males to produce (rather than a large repertoire) has not been investigated (as is the case in canaries *Serinus canaria*: Vallet & Kreutzer, 1995).

There is some evidence that quality of mimicry is correlated with male age in the satin bowerbird (Loffredo and Borgia 1986), which might lead to female preference for vocalisations that are complex and difficult to mimic. However, male satin bowerbirds mimic calls and not songs, and the calls they mimic do not appear to be very complex. There has been no explicit demonstration of learning although this has been implied for the more distinctive sounds, such as the laughing kookaburra-like noises that the bowerbirds produce. If these sounds are learned, it is not clear whether they are learned from the models or from conspecifics. Mimetic ability provides an indicator of male age in superb lyrebirds *Menura novahollandiae*, as subadults produce less accurate mimicry and have smaller repertoires than adults (Zann & Dunstan 2008). Although these data are consistent with mimicry playing a role in mate choice, alternative hypotheses cannot be excluded without explicitly testing the relationship between mating success and variation in mimetic quality and/or repertoire size.

In the only other species for which there has been an investigation into the relationship between mimicry and mating success, male black-browed reed warblers *Acrocephalus bistrigiceps* sing long, complex songs but do not achieve higher mating success (as measured by pairing date) when the mimetic component (syllables rather than whole songs) of their repertoire is higher (Dowsett-Lemaire 1979; Hamao and Eda-Fujiwara 2004).

In sum, then, the only data supporting the sexual selection hypothesis have come from bowerbirds and these are not especially compelling as yet. To determine that mimicry is preferentially used as a different and additional cue in female choice, both learning of sounds and specific benefits to using mimicry in displays still need to be demonstrated.

Social affiliation

The ability to match vocalisations of conspecifics for social cohesion has been reported in several species of birds and is likely to be prevalent in the taxa that learn their vocalisations (Cortopassi and Bradbury 2006; Vehrencamp et al. 2003; Hile et al. 2000). Robinson (1991) suggested that lyrebirds *Menura* spp. might use vocal mimicry in this kind of way, too, for maintaining contact in the dense rainforest in which they live. However, the value of using mimicry, rather than species-specific calls, to maintain contact is unclear. It may be that certain types of song transmit especially well in certain habitats and that it is more cost effective to copy these from the environment than it is to establish them as part of a species-specific repertoire. Structural adaptation for maximum transmission in each particular habitat appears to be the most suitable explanation for satin bowerbird vocalisations and, as Albert's lyrebirds (*Menura alberti*) mimic the calls of local satin bowerbirds, they, may too, produce effectively transmitted sounds (Putland et al. 2006; Nicholls and Goldizen 2006). However, this fails to explain why the lyrebirds mimic many more environmental sounds than just the most efficient call type. Importantly, models do not respond to lyrebird mimicry and there are, as yet, no data on the response by lyrebirds to mimicry produced by conspecifics.

Learning

In twenty-six years, then, almost no significant evidence supporting any of the functional hypotheses for vocal mimicry has been produced. Any of the data that do appear somewhat consistent with the predictions of one hypothesis or another are not convincing even for the hypothesis they have been invoked to support. And yet, the widespread existence and degree of accuracy of heterospecific vocal copying surely needs some kind of explanation. There is, however, one hypothesis that is consistent with almost all of the instances of vocal mimicry in songbirds.

In 1984, Hindmarsh suggested that, at least in the European starling (*Sturnus vulgaris*), avian vocal mimicry may be a result of mistakes made during song learning and therefore the mimicry serves no function. If mimicry is indeed a collection of sounds mistakenly picked up during song learning (during imprinting in some cases), rather than a result of specific context-dependent learning, we would expect one or more of the following: (1) mimetic repertoires to contain notes that are similar to the species-specific repertoire; (2) simple sounds to be mimicked more often than expected by chance; (3) mimetic repertoires should contain sounds that are commonly heard; (4) mimicry is not always used in the appropriate context.

In one of the few studies to test the predictions of more than one hypothesis, mimicry in robin chats *Cossypha* spp. is consistent with several predictions that come from the Learning Mistakes Hypothesis: robin chats are more likely to mimic simple songs and do not mimic significantly more predators or competitors (Ferguson et al. 2002). There was no correlation between model prevalence in the acoustic environment and presence or absence in the mimetic repertoire: many species that were commonly heard at study sites were never mimicked and several mimicked models were never heard at that site. However, the mimetic repertoire of the black-browed reed warbler (see above) does seem to be a reflection of the sounds of the common birds in their environment rather than of any specific group of species (Hamao & Eda-Fujiwara, 2004), as is that of the marsh warbler *Acrocephalus palustris* (Dowsett-Lemaire 1979).

There is at least one prediction that follows from the Learning Mistakes Hypothesis that could readily be tested: we would expect to hear mimicry often being used in inappropriate contexts. However, tests of the potential predictions will have to wait until we know more about what sounds are learned, how and if what context. For example, while it seems plausible that sounds that are similar to species-specific vocalisations are more likely to be learned in error than are dissimilar sounds, there is, as yet, little relevant evidence. The plausibility of such an idea is enhanced by findings such as the learning by song sparrows (*Melospiza melodia*) of swamp sparrow (*M. georgiana*) songs if the swamp sparrow syntax is edited to have a similar syntax to song sparrow conspecific songs (Marler and Peters 1988).

If mimicry is a result of making mistakes during song acquisition, then mimicry acquisition should be confined to the stages at which normal song learning occurs (Hindmarsh 1986a). This should be relatively straightforward to examine in closed-ended learners. With a relatively limited window of opportunity, closed-ended learners might also be expected to have small mimetic repertoires. Open-ended song learners, however, which modify their species-specific song repertoires after their first year of life, have greater opportunities to learn new sounds and may, then, learn more heterospecific songs by mistake.

The mimicry of alarm calling or of vocalisations of predatory species might also be explained through mistaken learning. This is because learning about any particular individual, location, object or event is always affected by the motivational state of the learner, which in itself is affected by stress. Although high acute stress (which itself may be good or bad) may make it difficult to recollect remembered information at the time, it is often correlated with good acquisition of information and long-term retention of that information (Rowe 2002). Hearing predators or alarm calls of other prey species is likely to increase stress levels acutely and may lead to enhanced uptake of lots of information pertinent to that instance. Not only would this lead to learning the specific sound, it may also lead to learning the context in which that sound was heard (Greenlaw et al. 1998). Such one-trial learning of complex information is the hallmark of learning to avoid unpalatable prey, imprinting, snapshot memory and, indeed, all episodic memory. Later production of a sound learned in a specific context may be expected to occur when the context is reproduced or when the animal is stressed. This would explain all of the apparent intentional insertion of mimicked alarm calls into alarm calling and mobbing in the appropriate context. As the neural structures underlying alarm call production are significantly different from those operating in song learning, it may also be the case that mimicry of song or complex sounds differs significantly in other ways from that of alarm calls.

As ten Cate (submitted) discusses, vocal learning may, in some cases, be the result of operant conditioning, whereby there is gradual acquisition in response to a reward. Mimicry by parrots such as Alex seems best explained in this way (Pepperberg 1981). Until we know more about the context in which mimicry is acquired, we cannot determine whether or not it is gradual or the result of a one-trial episode. Either of these explanations could lead to the apparent complexity of any one mimicked sound, or, both may be involved, which might explain the observation of a magpie mimicking a kookaburra two days after hearing a single call, and adding to its repertoire duetting kookaburras when exposed to these at a later date (Kaplan 1999).

Understanding the acquisition of mimicry could help to address associated questions such as choice of models. For example, reports of sedentary starlings mimicking species that are found many miles away seem best explained by the mimicry passing from one starling to another (Hausberger et al., 1991; P. J. B. Slater pers comm.). This process may also maintain mimetic calls across many generations, but not always: starlings, introduced to New Zealand in the 19th century are proficient mimics, but their mimetic repertoire does not contain calls from any non-introduced European birds (Hausberger et al. 1991). Once a mimicked sound is part of a bird's repertoire it may then be learned by a conspecific as part of the overall species-specific repertoire and, as such, would no longer be mimicry. Marsh warblers cease singing before their young hatch and repertoires are learnt entirely from heterospecifics, copied from species at both their European breeding grounds and Africa, where they over-winter (Dowsett-Lemaire 1979). Local mimetic 'dialects' of Albert's lyrebirds indicates vocalisations are learned directly from models, although the stereotyped sequence of different models produced during a mimetic bout suggests this component of mimicry is transmitted between conspecifics.

As yet we do not know whether any selectivity of model is accompanied by auditory or physiological constraints on models that are mimicked. Bill and vocal tract morphology are likely to limit the rate of syllable repetition and hence the type of models that a species is able to mimic (Podos 2001). For example, birds use both sides of the syrinx independently during song production, and mockingbirds (*Mimus polyglottus*) that produce more accurate mimicry use an identical motor pattern to their model species (Zollinger and Suthers 2004). When mimicking songs with notes outside their frequency range, mockingbirds either substitute a note within their frequency range, or omit the note. When notes are omitted other notes in the sequence are lengthened, so that the song is identical in duration to the model song, as if in recognition that song duration is important. When mimicking songs with high syllable repetition rates such as the canary *Serinus canaria*, mockingbirds cluster notes into discrete groups due to pauses for inspiration but, again, maintain the overall song length. In mockingbirds, at least, there may be physiological constraints on the accuracy of mimetic songs. By investigating these questions in other mimics, we would be able to examine whether species with smaller mimetic repertoires are physiologically constrained in the models that they mimic, or whether they have other constraints acting upon them. Captive rearing and deafening experiments can also provide valuable insights into the development and production of mimicry. As with species-specific song production, the roles of tape and live tutors and the importance of auditory feedback can be investigated (Kroodsma et al. 1997).

Conclusions

Twenty-six years on and we are no closer to determining even a single function for vocal mimicry. While this may, in part, be due to the relative paucity of work, there is only one study that has been carried out in this time that offers any credible support for the proposed functional hypotheses (indigobirds mimicking firefinches in a mate choice context). This view is consistent with the main outcome of a recent comparative analysis of vocal mimicry in Western Palearctic songbirds: there was no significant support for any of the proposed functional hypotheses but, importantly, those authors concluded that research effort is the best predictor of the existence vocal mimicry. I would add to this by concluding that future research effort should be directed towards determining the mechanisms underpinning the acquisition of mimicry and contexts of use.

Just as the following questions have been useful guides for directing research in song learning generally, we suggest that effort should be put into addressing them in the context of vocal mimicry: Is mimetic learning an open process with the potential for acquiring new vocalisations throughout an individual’s life, or is it restricted to specific periods? Does learning depend on refinement of sounds after repeated exposure, or can a sound be mimicked after a single hearing? Does an individual increase their quality or repertoire size as they age, thus providing information about their status? Do mimics learn directly from model species, indirectly from conspecific mimics or a combination of both? In what contexts is mimicry produced? Answers to these questions would help us go a long way to understanding just what avian vocal mimics are doing and the extent of their cognitive capabilities.

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