Vocal mimicry in the spotted bowerbird *Chlamydera maculata*

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"Of all living creatures… short of man himself,
bowerbirds are the most bizarre."

\- E. Thomas Gilliard

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Abstract

Vocal mimicry – the copying of heterospecific sounds – is a widely spread but poorly understood phenomenon. A fifth of all passerines are thought to mimic to varying extents but for most species all that is known is from anecdotal evidence. The bowerbird family (Ptilonorhynchidae) are well known for their mimicry with most species incorporating mimicked calls into their elaborate sexual displays. Spotted bowerbirds (*Chlamydera maculata*), despite being competent imitators, do not include mimicry in their displays. Here I discuss the vocal mimicry in this species, including suggestions of a possible function.

I considered evidence for four hypotheses previously put forward to explain vocal mimicry. I showed that, during observational studies, spotted bowerbirds preferentially mimic aggressive species and that the rate of mimicry also tends to increase in the presence of such species. This suggests that mimicry may be involved in threat avoidance, as a type of Batesian mimicry.

I tested this hypothesis using stuffed mounts of birds representing differing threats to the bowerbird. While there were some differences in species-specific vocalisation, such mounts did not appear to elicit a mimetic response. However, during experimental disturbances at the bower, some birds responded with an increased mimetic rate, supporting the threat avoidance hypothesis.

It was evident that there was individual variation in both species-specific and mimetic vocalisation. I explored this variation in terms of duration of bower tenure and individual status. I also examined different ways to estimate the complete mimetic repertoire size. I considered different mechanisms for learning mimicry and showed that bowerbirds do not mimic the most commonly heard birds at their bowers, or the same calls as their relatives or nearest neighbours.

Variation in bower design also occurs. I found no relationship between variation in bower quality and vocal characteristics. I found no evidence that bowers improve with duration of tenure or that there is cultural transmission of bower design among bower owners.

In summary, the most likely function of vocal mimicry in the spotted bowerbird is threat avoidance. However, I am unable to completely exclude other hypotheses.

Declaration

The text of this thesis is the result of my own research and contains no collaboration with the exception of the following:

1. Relatedness analysis (chapter 4) was carried out as part of a larger study with the assistance of Joah Madden, Tamsin Lowe, Hannah Fuller, Kanchon Dasmahapatra, Bill Amos and Francine Jury. This work resulted in the publication of two papers on which I am a co-author:

   Madden, J. R., Lowe, T., Fuller, H., Coe, R., Dasmahapatra, K., Amos, B. & Drury, F. 2004b. Neighbouring male spotted bowerbirds are not related, but do maraud each other. *Animal Behaviour*, **68**, 751 - 758.

   Madden, J. R., Lowe, T., Fuller, H., Coe, R., Dasmahapatra, K., Amos, B. & Dury, F. 2004c. Local traditions of bower decoration by spotted bowerbirds in a single population. *Animal Behaviour*, **68**, 759 - 765.

   These papers were not as a result of analyses carried out for my Ph.D. and are therefore not included in this thesis.

2. Joah Madden provided data on bower decorations and quality for the years 1998, 1999 and 2000 (chapter 6)

The text does not exceed 70,000 words. No part of this thesis has been submitted to any other university in application for a higher degree.

Rebecca L. Coe – July 2005

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Chapter 1. Introduction

Vocal mimicry, the copying of sounds typically of another species, is a widespread but poorly understood phenomenon. It occurs in disparate groups of animals: cetaceans, seals and, perhaps, elephants, but is most widely documented in birds (Chisholm, 1932; Ralls et al., 1985; Janik & Slater, 1997; Poole et al., 2005). Among passerines twenty percent of species are thought to mimic to some extent (Hindmarsh, 1984) although the parrots (order Psittaciformes) are the only non-passerine birds known to mimic (Cruickshank et al., 1993). Mimicry has fascinated scientists and laymen alike and anecdotal evidence of vocal mimicry abounds (e.g. (Chisholm, 1932; Vernon, 1973). From starlings mimicking mobile phones to Attenborough's footage of a lyrebird's uncanny mimicry of a chainsaw, vocal mimicry cannot fail to impress (Attenborough, 1998; Kendall, 2001). The talent of copying sounds has even been linked with the origin of human language but is curiously lacking in non-human primates (Fitch, 2000).

Despite this obvious interest, the phenomenon of vocal mimicry has suffered from what Dobkin (1979) described as "an appalling lack of experimental verification". Even now, vocal mimicry has been systematically studied in only a few species (*Phainopepla nitens*, (Chu, 2001a; Chu, 2001b); lyrebirds, *Menura* spp. (Robinson, 1974; Robinson, 1975; Robinson, 1991; Robinson & Curtis, 1996); mockingbirds, *Mimus polyglottos* (Howard, 1974; Owen-Ashley et al., 2002). Although parrots are renowned for their imitation in captivity (Chisholm, 1932), it was only a decade ago that they were discovered to mimic in the wild (Cruickshank et al., 1993) and the function of mimicry in this group is still not fully understood (Hile et al., 2000; Vehrencamp et al., 2003). The bowerbirds (Ptilonorhynchidae), justly famous for their bower-building behaviour, are, perhaps surprisingly, also accomplished mimics (Chisholm, 1932; Marshall, 1954). Here I investigate the occurrence and possible function of mimicry in the spotted bowerbird (*Chlamydera maculata*).

1.1 Definition of vocal mimicry

I follow Baylis' (1982) definition of avian vocal mimicry "as the resemblance of one or more vocalisations of an individual bird of one species either to the vocalisations typical of individuals of another species or to some environmental sound." From now on, I will refer to just "mimicry". The term "model" refers to the heterospecific or environmental sound that is mimicked.

Some authors have doubted that mimicry occurs at all, suggesting that resemblances between songs occur by chance or convergent evolution (e.g. Gordon 1932 as cited in Chisholm 1937; Laskey, 1944; Warham, 1962). For instance, species sharing the same acoustic environment may evolve similar calls because they are optimally transmitted in that environment (Morton, 1975; McGregor, 1991). However, this is not a widely held belief and it is generally assumed that a high degree of similarity, particularly of multiple models, is due to mimicry (e.g. Hindmarsh, 1984; Frith & McGuire, 1996; Kaplan, 1999; Cruickshank et al., 1993). In the case of the spotted bowerbird, the chances of vocalisations resembling around 14 other bird species by chance seems negligible, especially given the simplicity of its species-specific vocalisation in comparison to the calls it mimics (see sections 2.12 and 2.13).

It should also be noted that in saying, "a spotted bowerbird mimicked a whistling kite", I am not implying that the bowerbird heard the kite and then copied the call. This has been observed in other studies, including some in bowerbirds, and is referred to as "opportunistic mimicry" (Frith & Frith, 2004). I never observed this behaviour in the spotted bowerbird.

1.2 Function of vocal mimicry

Numerous functions for vocal mimicry have been proposed (Rechten, 1978; Dobkin, 1979; Baylis, 1982). Among the more fanciful suggestions are Oatley's mimicry of predators to warn young birds of their danger (1977 as cited in Kaplan 1999) and Chisholm's (1932) assertion that mimetic vocalisations are for "the most part expressions of pure *joie de vivre*".

I consider the possible functions of mimicry to divide into four main areas, listed below:

1) Interspecific communication – avoidance of threats and/or competitors

a) Beau Geste hypothesis

Krebs (1977) originally put forward the Beau Geste hypothesis to explain the occurrence of song repertoires. By singing many different types of (species-specific) song an individual gives a false impression that many individuals inhabit a territory, which might deter potential conspecific-competitors from entering. Although there is no strong evidence for this hypothesis in species-specific vocalisation (Yasukawa, 1981; Dawson & Jenkins, 1983; Haftorn, 1995), Rechten (1978) suggested it could also apply to vocal mimicry, particularly in territorial birds. The mimicry could deter territory-seeking individuals of species other than the model, either conspecifics of the mimic or other competing species.

There is some anecdotal evidence to support this notion. For example, some species incorporate heterospecific mimicry into their territorial advertisements (Curio, 1978), which might function to deter heterospecific competitors. Additionally, Brenowitz (1982) found that red-winged blackbirds (*Agelaius phoeniceus*) did not appear to distinguish between playback of conspecific song and isolated mockingbird (*Mimus polyglottos*) mimicry of the same calls, responding aggressively to both. However, subsequent tests in which the mimicry was embedded in mockingbird song, as occurs naturally, failed to replicate these findings (Owen-Ashley et al., 2002).

As has been found when investigating Beau Geste as an explanation for repertoire size (i.e. Yasukawa, 1981), it is difficult to formulate predictions that are unique to this hypothesis. For example, one prediction of the Beau Geste hypothesis is that the vocalising bird will change perches between bouts of different song types to enhance the illusion of multiple occupants of a territory. However an alternative explanation is that flying to a new perch delays the delivery of the next song, and this increases the likelihood of a change in song type (Hinde, 1958). In the case of vocal mimicry, tests to observe whether heterospecific competitors are more likely to be deterred by playback of a large mimetic repertoire versus a small mimetic repertoire would be consistent with the Beau Geste hypothesis (Rechten, 1978). This result would also be consistent with the habituation hypothesis (Hartshorne, 1956), under which several call types might be more effective than a single call type at deterring intruders because the receiver is less likely to become habituated.

b) Batesian acoustic mimicry

In the same way that a palatable species may avoid predation by visually resembling a noxious species (Bates, 1862), avian mimics may deter would-be predators or competitors by copying the calls of predatory or aggressive birds (Dobkin, 1979). Similar to the Beau Geste hypothesis, the intended receivers of Batesian mimicry are likely to be heterospecific competitors. These perceive a threat from the would-be predator, avoid entering the territory of the mimic, and thus do not compete for its resources (competitive Batesian acoustic mimicry *sensu* Dobkin, 1979; see also Harcus 1977; Kaplan, 1999). Alternatively, the intended receivers may be potential predators. These are deterred from attacking the mimic in order to avoid a costly encounter with another predator (Vernon, 1973; Dobkin, 1979), or are perhaps confused by the conflicting acoustic signals coming from the mimic (Harcus, 1977; Curio, 1978). Chisholm (1937) thought that the use of heterospecific calls to deter predators was "hopeless", although this appears to be because he thought it evoked conscious deception.

Evidence for vocal mimicry reducing interspecific competition is mixed (i.e. mockingbirds, (Howard, 1974; Brenowitz, 1982; Owen-Ashley et al., 2002) see above). Harcus (1977) claimed that the high incidence of vocal mimicry during the breeding season of models, when they were also vocally most active, was evidence that the function of mimicry was to interfere with heterospecific communication. However, there was no discussion of the effect mimicry had on the models, or how such interference, if it existed, would benefit the mimic. Such mimicry of common calls might also be caused by mistakes made during song learning (see below).

There is a lot of anecdotal evidence for Batesian acoustic mimicry, in particular in nesting females protecting eggs or nestlings (e.g. Chisholm 1937; Warham, 1962; Morton, 1976). There are also reports that two species of birds mimic rattlesnakes in the presence of potential predators (pale-breasted spine tail *Synallaxis albescens*, Staneck 1999; burrowing owls *Athene cunicularia*, Owings et al., 2002). Kaplan (1999) reported Australian magpies (*Gymnorhina tibicen*) mimicking potential nest predators the barking and boobook owl. However, in his extensive review of avian vocal mimicry, Dobkin (1979) concluded that bowerbirds were the only group to display Batesian acoustic mimicry, in its traditional sense of predator, rather than competitor, avoidance.

If the function of vocal mimicry were that of avoidance of threats or competitors by aposematic signalling, mimics would be expected to preferentially mimic aggressive or predatory birds and to mimic more often in the presence of potential predators or competitors. Despite numerous observations and some testable predictions, this hypothesis has not been experimentally verified (K. Munro and J. R. Madden pers comms.; Frith & Frith, 2004). There has been no test of receivers' reaction to mimicry in this context although there is anecdotal evidence that starling-predators take no notice of the starlings' mimicry of predators (Kaplan, 1999).

c) Intervention by a third species

Mimics might induce mobbing of predators by the model species. Morton (1976) described being mobbed by yellow-green vireos (*Vireo flavoviridis*) after a female thick-billed Euphonia (*Euphonia laniirostris*), sitting on her nest, mimicked its alarm calls. Although this function of mimicry has not been substantiated experimentally, the phainopeplas (*Phainopepla nitens*) mimic the alarm calls of other species when distressed (e.g. when captured in mist nets) and this does elicit mobbing by heterospecifics. However, playback experiments demonstrated that phainopeplas species-specific alarm calls evoked a stronger mobbing response amongst heterospecifics than mimicry of their calls (Chu, 2001a; Chu, 2001b).

It has been suggested that alarm calls, including mimetic ones, may attract a secondary predator, possibly coming in search of injured prey, giving the caller a chance to escape during the ensuing scuffle with the first predator (Curio, 1978; Hogstedt, 1983). Chu found no evidence that mimicry of alarm calls attracted a second predatory species (Chu, 2001b).

2) Intraspecific communication - sexual selection

The songs of many birds are complex, with large and varied repertoires. This complexity can be important either in territorial interactions between males or in attracting a female (Catchpole & Slater, 1995). Males with the largest repertoire size pair earlier (Catchpole, 1980; Eens et al., 1991), have larger and better quality territories (Hiebert et al., 1989; McGregor et al., 1981), more mates (Eens et al., 1991) and greater lifetime reproductive success (Hiebert et al., 1989). One, and perhaps the simplest, way to increase repertoire size is to incorporate the calls of other birds (Howard, 1974). Although Robinson (1974) claimed that mimicry would be unlikely to occur in courtship displays due to the need for species recognition, unless, as in lyrebirds (*Menura* spp.), mimicry is delivered in a "species-specific" style.

Howard (1974) was the first to show that male birds with the most elaborate songs (large repertoires, with both species-specific and mimetic elements) obtained mates earlier than males with simpler songs, which in turn correlates with reproductive success. He studied this in a wild population of mockingbirds (*Mimus polyglottus*) – a proficient mimic, as the name suggests. He did not find any territorial function for the mimicry and suggested that its sole function was to increase repertoire size. Others have also suggested this (Marshall, 1950; Dobkin, 1979,) but there is still no empirical evidence of the *mimetic* repertoire being correlated to mating success. Indeed, two studies have failed to find a link between mimetic repertoire size and pairing date (*Acrocephalus palustris*, Dowsett-Lemaire, 1979; *A. bistrigiceps*, Hamao & Eda-Fujiwara, 2004).

The quality and quantity (in terms of length of bout) of mimicry appears to be correlated with mating success in the satin bowerbird (*Ptilonorhynchus violaceus*). The males in this population only mimicked two models so variation in repertoire size was not investigated (Loffredo & Borgia, 1986). The occurrence of mimicry in the courtship displays of other bowerbird species is also consistent with it playing a role in sexual selection (e.g. tooth-billed bowerbirds, *Scenopoeetes dentirostris*, Frith & McGuire, 1996; Archbold's bowerbird, *Archboldia papuensis*, Frith et al., 1996) but links between mimicry and mating success have not been tested.

Mimetic vocalisation 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 & Borgia, 1986; Slater, 2003). This might lead to female preference for calls that are difficult to mimic because they are complex or rare in the sound environment. Females have been shown to prefer species-specific songs that are energetically demanding for males to produce (Gibson & Bradbury, 1985; ten Cate et al., 2002; Gil & Gahr, 2002; Ballentine et al., 2004), the same may be true of mimetic calls. Alternatively, females might demonstrate a preference for novelty;

incorporating heterospecific song into display is a way of achieving this (ten Cate & Bateson, 1988).

3) Intraspecific communication - Social affiliations

a) Phatic communication

Robinson (1977, 1991) suggested that vocal mimicry in the lyrebirds (*Menura* spp.) might be important for individuals to maintain contact in the dense rainforest habitat. Unlike species-specific calls, mimetic calls convey no particular message of aggression, courtship or alarm to other lyrebirds. Robinson termed this "phatic communication". About three quarters of the superb lyrebirds' (*M. novaehollandiae*) vocal display is mimetic but mimicry is interspersed with species-specific calls, which would allow receivers to determine the sender's species and status (Robinson, 1991; Owen-Ashley et al., 2002). Robinson suggested this could be the function of mimicry in other sociable mimics, like European starlings (*Sturnus vulgaris*) and Australian magpies (*Gymnorhina tibicen*), but this suggestion remains to be tested.

b) Individual recognition

Individual recognition could be achieved if individuals had different mimetic repertoires. For example, Harcus (1977) was able to identify individual chorister robins in this way, although did acknowledge that this required listening to an individual for extended periods. Neighbouring male starlings seem actively to avoid using the same loud mimicries as each other, potentially enabling females to recognise them at a distance (Hausberger et al., 1991). Individual recognition is important in colonial species, like starlings, to prevent costly aggression against more dominant individuals (Feare, 1996). Individual recognition by different mimetic repertoires has also been suggested in *Cacius cela* (Feekes, 1982). In none of these species has the ability to recognise conspecifics by mimicry been tested and it is unclear why mimetic vocalisations would be used in preference to species-specific ones, unless perhaps the species-specific song was very simple (Nottebohm, 1972; Dowsett-Lemaire, 1979; Hindmarsh, 1986).

c) Call convergence

The ability to accurately mimic heterospecific calls may arise from call convergence. This behaviour has been observed in several species of birds (Nowicki, 1989; Trainer et al., 2002; Vehrencamp et al., 2003) as well as in cetaceans (Miller et al., 2004; Mercado et al., 2005). Paired budgerigars (*Melpsittacus undulateus*) develop shared calls shortly after being housed together and furthermore the male's contact call converges on that of his mate suggesting vocal imitation is important in pair bonding (Hile et al., 2000). Orange fronted conures (*Aratinga canicularis*) also have the ability to converge on other individuals' contact calls, perhaps signalling social affiliation to potential flock mates (Vehrencamp et al., 2003). Species-specific call convergence might lead to heterospecific mimicry, especially in captivity (see also learning mistakes below, Cruikshank et al., 1993; Hile et al., 2000).

Vocal matching of heterospecific mimicry has also been observed (Harcus, 1977). Harcus played chorister robin (*Cossypha dichroa*) mimicry and noted that conspecifics would respond by mimicking the same model. This may have the same territorial function as matched counter-singing in species-specific song, where it appears that a male hearing a song that is closely matched to his own will be less likely to invade that neighbour's territory (Bertram, 1970; Catchpole & Slater, 1995). It is not clear why the chorister robin would use mimicry in matched-counter singing rather than species-specific vocalisation.

4) Learning Mistakes hypothesis

The Learning Mistakes hypothesis states that mimicry is a non-functional by-product of the ability to learn complex song. It was first formalised by Hindmarsh (1984, 1986) but had been hinted at by several previous authors (reviewed by Chisholm, 1937). Hindmarsh suggested that mistakes made during learning are the probable causal explanation for mimicry in the European starling (*Sturnus vulgaris*) and that the mimicry serves no function. However, whilst the species-specific song of the starling has been the subject of substantial research (West et al., 1983; Cuthill & Hindmarsh, 1985; Riters et al., 2000), there have been no experiments to test whether mimicry truly serves no function in this species. As repertoire size is correlated with mating success, mimicry might be important in increasing this (Eens et al., 1991; Mountjoy & Lemon, 1996). Observations from other species have also been consistent with the learning mistakes hypothesis, although other hypotheses could not be completely excluded (robin chats, *Cossypha* spp., Ferguson et al., 2002; black-browed reed warbler, *Acrocephalus bistrigiceps*, Hamao & Eda-Fujiwara, 2004).

Vocal mimicry is often observed when individuals are reared away from conspecifics (Pepperberg, 1985; Poole et al., 2005). Here, it seems that the learning mistakes hypothesis does explain the occurrence of mimicry. In an impoverished sound environment birds, particularly young ones, will learn heterospecific vocalisations (Cooper & Murphy, 1984; Kaplan, 1999). This is especially true if there is social interaction between the different species (Baptista & Morton, 1981; Baptista & Petrinovich, 1984). There are numerous accounts of captive species (birds and others) mimicking their human captors (Bertram, 1970; West et al., 1983; West & King, 1990; Ralls et al., 1985; Pepperberg & Schinke-Llano, 1991; Kaplan, 1999). However, it seems that these are exceptional circumstances and whilst some mimicry in wild animals might be explained by mistakes made during learning, it seems an unsatisfactory explanation for many consistent mimics. This is especially true of proficient mimics that do not sing, and might not learn their species-specific calls (e.g. parrots, Cruickshank et al., 1993, and hill mynahs, *Gracula religiosa,* Bertram, 1970; Catchpole & Slater, 1995).

Song in birds varies greatly between species in organisation (i.e. whether songs are sung with continuous or eventual variety) complexity, function and how and when it is learnt (Catchpole & Slater, 1995; Beecher & Brenowitz, 2005). It seems possible that the form and function of mimicry might also vary considerably across species. The above hypotheses may each explain the function of mimicry in one or more species, but are not mutually exclusive. For example, mimicry may discourage heterospecific intruders (Batesian mimicry or Beau Geste hypothesis) but may simultaneously act as an indictor of male quality to a potential mate (sexual selection hypothesis). However, the function of vocal mimicry has been experimentally investigated in very few species (phainopeplas Chu, 2001a; mockingbird Owen-Ashley et al., 2002).

1.3 Acquisition of vocal mimicry

The process by which vocal mimicry is acquired is probably even more poorly studied than its function (Dobkin, 1979), which is perhaps surprising as the acquisition of bird song in general has been so well studied (Catchpole & Slater, 1995). Indeed, previous work on species-specific song perhaps makes the phenomenon of vocal mimicry even more puzzling. Marler and Peters (1977) demonstrated that juvenile swamp sparrows (*Melospiza georgiana*) were able to pick out and copy only the conspecific calls from recordings mixed with the song of the closely related song sparrow (*M.melodia*). If such an accurate distinction can be made between conspecific and heterospecific, it is not clear why some birds mimic the calls of many, distantly related species, some of which are not even avian. Hindmarsh (1986) suggested that for birds with very complex songs having a template for conspecific song only would be too costly, hence mistakes are made in song learning that cause similar heterospecific songs to also be copied.

If mimicry is a result of making mistakes during song acquisition the process for mimicry acquisition should be identical to normal song learning (Hindmarsh, 1986). However, there is a lot of variation in conspecific song learning among species (Catchpole & Slater, 1995; Beecher & Brenowitz, 2005). Some species appear to learn all their song during a "sensitive period" early in life (closed-ended learners, e.g. song sparrows, Marler & Peters, 1987) whilst others are open-ended learners, and can continue adding to and modifying their songs throughout their lives (e.g. canaries, *Serinus canaria,* Nottebohm & Nottebohm, 1978). Recent research suggests this division might be artificial and most songbirds can achieve a degree of modification beyond the sensitive period (White & Mooney, 1999). Presumably the process of learning mimicry is just as varied as species-specific song learning.

A distinction has been made in the literature between mimetic calls transferred between conspecifics and mimicry learnt directly from the model (Dobkin, 1979), although this division is also rather artificial as the mimicked call is originally copied from the model. The distinction, therefore, is more whether mimicry is most commonly copied from conspecifics or from heterospecific models.

Evidence for mimicry being transferred among conspecifics comes from the European starling. There have been several reports of sedentary starlings mimicking birds that are only found many miles away (Hausberger et al., 1991; P. J. B. Slater pers comm.). The suggested explanation for this is that the mimetic call has been passed from starling to starling. However, this process does not appear to maintain mimetic calls across many generations: starlings that were introduced to New Zealand over a century ago are proficient mimics but their mimetic repertoire does not contain calls from any European birds (Hausberger et al., 1991). There is, however, structural similarity between mimetic calls of New Zealand and European populations of starlings that Hausberger et al. took to be evidence for genetic inheritance of a template for suitable models. Local variants in mimetic calls also suggest that mimicry can be learnt from conspecifics (Eens et al., 1992) and mimetic vocalisations in both the lyrebird (Robinson & Curtis, 1996) and the mockingbird (Howard, 1974) appear to be culturally transmitted among conspecifics.

Others have assumed mimicry is learnt directly from models, perhaps suggesting a different mechanism from species-specific song learning (Chisholm 1932). Witchell (1896 as cited in Baylis, 1982) argued that vocal mimicry was evidence that song, in general, was learnt and birds could acquire new elements from the acoustic environment. Captive individuals certainly can learn new mimetic sounds. For example, Kaplan (1999) reported how a captive Australian magpie altered its mimicry of a solitary kookaburra in an adjacent aviary to the chorus of a pair of kookaburras when a second individual was added. In an extreme natural example, the marsh warbler's (*Acrocephalus palustris*) large repertoire is believed to consist only of mimicked elements, copied from species at both their European breeding grounds and Africa, where they over-winter (Dowsett-Lemaire, 1979). Vocalisation in these birds is learnt entirely from heterospecifics because conspecifics have ceased singing before the young hatch.

The particular models mimicked by a species might be determined, as suggested above, by the function of mimicry. For example, if a species incorporates mimicry into its vocalisation to scare off potential predators (Batesian acoustic mimicry) it will preferentially mimic predators. However, there are also anatomical limitations to the models that are mimicked. Kaplan (1999) noted that the captive Australian magpies did not mimic pardalotes (*Pardalotus* spp.) or fairy wrens (*Malurus* spp.), despite these being vocal, frequent visitors to the garden surrounding the aviary, because the calls of these birds were beyond the frequency range of the magpies. Bill and vocal tract morphology might also limit the rate of syllable repetition and hence the type of models that a species is able to mimic (Podos, 2001; Podos et al., 2003).

As with the function of vocal mimicry there are few studies that investigate the mechanism of learning vocal mimicry. Possible exceptions are in the Australian magpie (Kaplan, 1999) and European starling (Hausberger et al., 1991; Eens et al., 1992).

1.4 Vocal mimicry in the bowerbird family (Ptilonorhyncidae)

There are 20 species of bowerbird, all endemic to Australia and Papua New Guinea. They are best known for their bower building behaviour: males construct and decorate elaborate structures of various shapes in order to attract a mate. This unusual behaviour has made the bowerbirds the subject of many studies on sexual selection (e.g. Borgia, 1985a; Madden, 2001b; Coleman et al., 2004) and perhaps because of this the bowerbirds' impressive mimetic ability has been largely over-looked. Mimicry has been reported in all bowerbird species except for the three species of monogamous catbirds (*Ailuroedus* spp.). The catbirds are generally considered ancestral to the other bowerbirds and do not build a bower or display court (Chisholm, 1932; Kusmierski et al., 1997; Frith & Frith, 2004). Mimicry is observed in bowerbird sexual displays, bower advertisement calls and in nest and bower defence.

Bowerbird mimicry often includes not just calls of other birds, but also the sound of fluttering wings, cicadas, dogs, human speech and sounds from inanimate sources, like the crack of a stock whip and dripping water (Frith & Frith, 1993; Frith & Frith, 2004). Some species, including spotted bowerbirds, make plaintive cat-like calls. There is on-going debate about whether this is mimetic, or a species-specific call – perhaps a relict from their common ancestry with the catbirds, so-called because of their distinctly feline voice (Frith & Frith, 2004). One author claimed it was a "natural" note as a juvenile satin bowerbird raised in captivity uttered these cat-calls despite never encountering a cat, however, it was possible that the bird had learnt them from its mother (North, 1901; as cited in Frith & Frith, 2004).

In all polygynous species (i.e. excluding the catbirds), except the grey bowerbirds (*Chlamydera* spp.), mimicry is observed during courtship displays (e.g. Frith & Frith, 1993; Frith & McGuire, 1996; Frith & Frith, 2000). Satin bowerbirds (*Ptilonorhynchus violaceus*) include mimicry of up to five species in the quiet subsong they perform to females at the bower. Loffredo and Borgia (1986) found that the quality of this mimicry, as measured by a subjective score for the structural integrity (high score for mimetic songs of pure tonal structure, lacking interruptions of other sounds by the singer), improved with male age. Older males also sang longer bouts of mimicry. These two features of courtship song were positively correlated with mating success (Loffredo & Borgia, 1986). Tooth-billed bowerbirds (*Scenopoeetes dentirostris*) are masterful mimics, the reported repertoire of this species includes up to 44 bird species, as well as bats, frogs and cicadas, although local cultures appear to exist so that no single bird has such an extensive repertoire (Frith & Frith, 2004). Tooth-bills commence their courtship with long medleys of 10 or more mimicked calls, the quality of which Frith and McGuire (1996) predict should also be positively correlated with mating success and male age.

Marshall (1950) suggested that continuous vocalisation in display was essential in the dense vegetation of rainforests, the likely habitat of ancestral bowerbirds, where visual displays would be restricted. Mimicry could provide a constant stream of sounds to advertise the location of a bower site, whilst perhaps avoiding signals of aggression conveyed by species-specific vocalisation (Robinson, 1991), However such "phatic communication" is more likely in social birds, like lyrebirds, where communication besides that during courtship is important. In the grey bowerbirds in particular, their current open habitat might reduce any need for continual acoustic signal.

It seems plausible that *courtship* mimicry in bowerbirds is sexually selected (see 1.2). Robinson (1974) suggested that bowerbirds mimic the calls of predatory birds to enhance the aggressive nature of their sexual display. Mimicry in courtship display may provide an honest indicator of male quality and/or age. If, as suggested by Loffredo and Borgia (1986), mimicry requires learning and practice over a number of years, young males would not be able to "cheat" and this might explain their observed correlation between mimetic quality and mating success.

Most bowerbirds advertise the location of their bowers with loud, harsh calls given from a habitual perch. Some species have been observed to incorporate mimicry into this advertisement song (Marshall, 1950; Gilliard, 1969; Frith &

McGuire, 1996; Frith & Frith, 2004). This may be to attract females to a bower or to indicate male attendance at bowers both to potential mates and rivals (Frith & Frith, 2004). The mimetic content of these calls might simultaneously demonstrate male quality, although this idea has not been tested.

Finally, mimicry has been observed when females at nests or males at bowers have been disturbed (see also 1.5 below). Mimicry in this context has been observed in four species of grey bowerbirds, including spotted bowerbirds, and also in satin bowerbirds (*Ptilonorhynchus violaceus*) and often seems to include mimicry of aggressive species (Warham, 1962; Frith & Frith, 2000). This appears to be a form of defence and is possibly an example of Batesian acoustic mimicry (Dobkin, 1979).

Little is known about how bowerbirds acquire their vocalisation, both mimetic and species-specific. Oscines, members of the sub-order Passeri, (to which bowerbirds belong) generally learn their song (Brenowitz, 1982). However, calls, which are typically shorter, simpler and produced year round, by both sexes (Catchpole & Slater, 1995) are often unlearnt (McGregor, 1991; ten Cate et al., 2002). The species-specific vocalisations of the bowerbird fit these criteria and may therefore be unlearnt calls (although it should be noted that the distinction between song and call might be arbitrary (Catchpole & Slater, 1995)). It is not unknown for birds that do not learn their own vocalisations to be highly competent mimics. Neither the parrots (Psittaciformes) nor the hill mynah (*Gracula religiosa*) are thought to learn their species-specific vocalisations and yet are striking mimics (Bertram, 1970; Catchpole & Slater, 1995).

Mimetic vocalisation in bowerbirds could be learnt directly from the models or from conspecifics, perhaps being culturally transmitted among neighbouring bower owning males. This latter pattern of learning is observed in species-specific song learning in many birds (McGregor, 1991). It is also conceivable that bowerbirds learn mimicry from their mothers as nestlings (Warham, 1962). There is no record of mimetic repertoire changing during the lifetime of a bowerbird but the improvement of mimetic quality in older satin bowerbirds (Loffredo & Borgia, 1986) suggests it might be possible.

1.5 Vocal mimicry in the spotted bowerbird (*Chlamydera maculata*)

Unlike the other bowerbirds, the grey bowerbirds (the five species in the genus *Chlamydera*) do not typically incorporate mimicry in their sexual displays or bower advertisements (Frith & Frith, 2004; although see Marshall, 1954). In 551 sexual displays in the spotted bowerbird, not one was observed to include mimicry (J. R. Madden pers comm.). This is not to say grey bowerbirds, including spotted bowerbirds, are not accomplished mimics. Indeed, Chisholm (1932) praised them as the "finest non-singing mockers in the world". Spotted bowerbirds mimic around 16 avian models as well as mimicking human speech, dogs and other environmental sounds, like emus twanging fence wire (Frith & Frith, 2004). These may be in sharp contrast with its harsh, grating, species-specific calls (Marshall, 1954).

In the spotted bowerbird (and the other grey bowerbirds) mimicry, especially of predatory species, has been observed when a nesting female is disturbed (Warham, 1962; Frith & McGuire, 1996). The female may also feign injury to divert attention from her vulnerable nest (Marshall, 1954). Mimicry is commonly observed when humans disturb birds at their bowers, and here, too, there are reports of bowerbirds mimicking aggressive species (Marshall, 1954; Frith & McGuire, 1996). Chisholm (1932) noted that in contrast to lyrebirds, the mimicry of the spotted bowerbird was delivered at the same amplitude as the models' calls and could perhaps be deceptive. He was quick to point out he did not mean the calls were "deliberate", suggesting that as most of the spotted bowerbirds calls were mimetic, these were the only calls available to a distressed female on her nest.

Dobkin (1979) concluded that spotted bowerbirds, as well as satin bowerbirds, were capable of Batesian acoustic mimicry (see 1.2). Whilst there are no reports of predators being deterred by mimicry, Marshall (1950) reported that a spotted bowerbird's mimicry of a whistling kite was accurate enough to cause a hen and her chicks to seek cover (see also Chisholm, 1937). Marshall (1954) also noted that the current function of mimicry might not be the same as its original function. Ancestors of the spotted bowerbirds could also have mimicked during their courtship display, only to discard this custom once they inhabited more open woodland where visual signals might be more effective. The vocal mimicry might now play another role.

There has been a single experiment designed to determine whether Batesian acoustic mimicry explained spotted bowerbird mimicry, and this failed to find any supporting evidence (see chapter 4; K. Munro and J. R. Madden pers comms.). No other systematic studies on the occurrence or function of vocal mimicry in the spotted bowerbird have been conducted.

1.6 Bowerbirds and their bowers

In 1985, Borgia (1985b) first demonstrated that features of the bower were correlated with mating success. Since then similar links have been shown in other species of bowerbird (spotted bowerbird, Madden 2001b; Madden 2003a; Macgregor's bowerbird, *A.macgregoriae*, Pruett-Jones & Pruett-Jones, 1983; regent bowerbird, *Sericulus chrysocephalus*, Lenz 1994 and Vogelkop bowerbird, *A.inornatus*, Uy & Borgia, 2000). However, it is not known how measures of bower quality relate to other measures of male quality, including vocalisation characteristics. There is a general lack, not just in bowerbirds, of knowledge on how different aspects of multi-component signals inter-relate (Johnstone, 1995; Johnstone, 1997; Rowe & Skelhorn, 2004). Theoretical work predicts that different features of quality might be correlated (Johnstone, 1995) and this is supported by empirical evidence in the satin bowerbird where there is a positive correlation between male UV plumage colouration and measures of bower quality (Doucet & Montgomerie, 2003). It is conceivable that measures of vocal quality – for instance mimetic repertoire size – might also correlate with bower quality or other indicators of male quality. However, it is also possible that different components of male display signify different aspects of quality ("multiple messages" hypothesis Johnstone, 1995), which might not necessarily correlate with each other.

Although much more is known about bowers and their function than about bowerbird vocalisation, there are still considerable gaps in our knowledge. Surprisingly, especially considering Borgia's long-term data set on the satin bowerbirds of Wallaby Creek (Borgia, 1985a; Coleman et al., 2004), to date there are no studies following the change in bower decoration and quality over a male's life. A long term study revealed changes in male parasite load over nine years (Borgia & Collis, 1989; Collis & Borgia, 1993) and another showed that measures of bower quality were highly repeatable over a two year period (Borgia, 1995a). Although many authors have asserted that bower construction has a learnt component (Vellenga, 1970; Borgia and Collis, 1993; Maxwell 1999 as cited in Madden, 2001a) this remains untested. In several species of sexually dimorphic bowerbirds (e.g. satin bowerbird *Ptilonorhynchus violaceus*; regent bowerbird, *Sericulus chrysocephalus*) the males retain a juvenile, female-like plumage until they around 5 or 6 years old (Frith & Frith, 2004). Collis and Borgia suggested this delayed plumage maturation allows young males to visit adults' bowers and observe bower building and display without being harassed (facilitated learning hypothesis Collis & Borgia, 1992). In spotted bowerbirds, which are sexually monomorphic, the size of the lilac nuchal crest tends to be smaller in non-owner males and is perhaps a similar, although very subtle, badge of status (Madden et al., 2004a). Others have observed that young males build poorer quality and sparsely decorated bowers (Pruett-Jones & Pruett-Jones, 1983; Diamond, 1986; Frith & Frith, 2004). Bower quality might therefore be expected to improve with the duration of bower ownership, but this has not been tested.

The similarity of neighbouring bowers suggests there is cultural transmission amongst bower owners (Diamond, 1986; Madden et al., 2004c). This might also provide a mechanism for mimicry being transferred among conspecifics. Geographically close bowers are more likely to display the same type of decorations than more distant bowers, and this is not caused by neighbouring males being related, or due to local availability of decorations (Madden et al., 2004c). Diamond (1988) suggested two mechanisms that could explain these local traditions in bower design. Firstly, males observe and copy features of neighbouring bowers or, secondly, males respond to differences in local female choice. Neither of these mechanisms has been experimentally verified.

1.7 Aims of thesis

a) To determine which species the spotted bowerbird mimics: do they preferentially mimic predators, competitors or common, simple calls? Determining this would provide evidence for or against the Batesian mimicry, Beau Geste or Learning Mistakes hypotheses. For example, if common, simple calls are mimicked more often this would be consistent with the Learning Mistakes hypothesis.

b) To determine whether mimicry occurs in the presence of competitors, predators or conspecifics. Does the amount of mimicry change throughout the season? Again, this knowledge of the natural occurrence of mimicry would provide data so as to discriminate between the Beau Geste, Batesian mimicry, Learning Mistakes or sexual selection hypotheses. For example, increase in mimetic rates in the presence of conspecifics and towards the mating season would suggest that mimicry was a sexually selected display.

c) To experimentally test some of the predictions given by the vocal mimicry hypotheses. Firstly, to determine whether mimetic rate increases in the presence of mounts of predators or during disturbances at the bower, as is predicted in the Batesian mimicry hypothesis. Secondly, to investigate individual differences in vocalisation, including mimetic repertoire, and mimetic and species-specific call rate, and then to use these differences to determine whether males appear to learn mimicry from neighbours or related individuals.

d) To investigate the relationship between vocal traits and bower characteristics that indicate male quality with the prediction that correlation between the two suggests a sexually selected function for vocalisations.

e) To explore the variation in bower quality over a number of years: do bowers improve with increasing duration of bower ownership as would be expected if they have a large learnt component and are honest indicators of male age/experience.

f) To consider the affect of cultural transmission on the design of bowers with the expectation that neighbouring bowers might be more similar than more distant ones because males track the changes in each other's bowers. Also to test whether preferences for novel decorations are influenced by seeing them at rivals' bowers.

Chapter 2. General Methods

2.1 Study species

The spotted bowerbird (*Chlamydera maculata* Gould) is a medium sized passerine bird, measuring around 27 to 31 cm from bill to tail (Simpson & Day, 1999). It is distributed throughout central Queensland and central New South Wales and into the extreme northwest of Victoria and South Australia (Frith & Frith, 2004). Its plumage is mainly cryptic brown, with yellowish spots dorsally and a fawn, subtly streaked breast. This species' most distinctive feature is a bright pink nuchal crest, which is erected during displays (see fig 2.1 a and b). Spotted bowerbirds are sexually monomorphic, although females, non-bower owning males and juveniles tend to have a smaller or non-existent crest (Madden et al., 2004a). Spotted bowerbirds are primarily frugivorous but the diet is supplemented with some invertebrates. Like other members of the bowerbird (Ptilonorhynchidae) family, male spotted bowerbirds construct a bower that is used to display to rival males and to potential mates.

Fig 2.1: a) The back of a spotted bowerbird, note the pink crest and the coloured leg bands (see section 2.6), this individual is OY-GBR **b)** spotted bowerbird at bower.

2.2 Study site

The main study site was Taunton National Park, a scientific national park just outside of the town Dingo, about 200km west of Rockhampton, Queensland (23.54989 S and 149.24088 E, see fig 2.2a and b and fig 2.6). Taunton was formed from two cattle properties in 1986 after the discovery of a population of bridled nailtail wallabies (*Onychogalea fraenata* see fig 2.3), a species thought to have been extinct since the 1930s. The park is now managed to encourage the survival of the nailtail wallaby with measures including baiting for non-native predators (cats, dogs and dingoes) and weed control. It is not open to the general public.

The park consists of 11,626 hectares of a complex mosaic of acacia, predominantly brigalow (*Acacia harpophylla*), and eucalypt communities and a combination of pristine woodland and cleared grazing land. There are 13 artificial dams on the park and numerous seasonal creeks. The park is well serviced with access tracks, except after heavy rain when many of these become impassable.

Access to the park was kindly allowed by Queensland Parks and Wildlife Service (permit numbers: C6/000199/02/SAA, WISP01151003 and WITK01150903).

Three bowers were also studied on the neighbouring cattle properties of Eldeebar (23.42742 S and 149.29184 E) and Araluen (23.44124 S and 149.37304 E). Permission to use these sites was kindly granted by the Dowe family and Lindsay Barlow respectively.

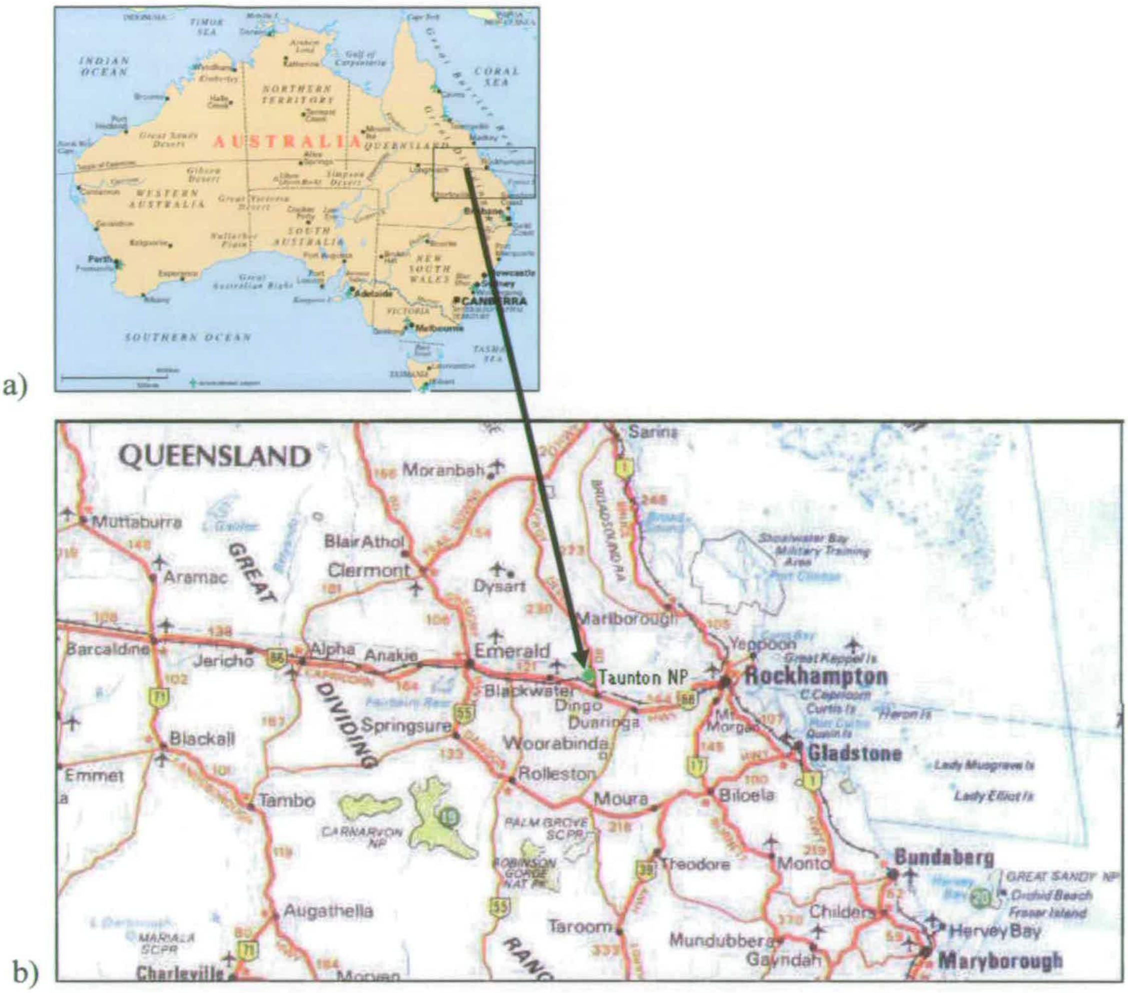


Fig 2.2: **a)** Map of Australia and **b)** detail of Central Queensland, including Taunton National Park

Fig 2.3: Bridled nailtail wallaby *Onychogalea fraenata*

2.3 Field seasons

Two visits were made to the study site, between 28th May and 15th October 2002, and 18th June and 26th November 2003. These dates were chosen to coincide with the beginning of the bower maintenance season, however at the start of the first field season the bowerbirds were not very active at the bowers so a decision was made to start the second season later.

In addition, Dr Joah Madden kindly made data available to me from his three previous field seasons at Taunton in 1998, 1999 and 2000, including GPS positions, and details of bower ownership and bower decorations (for more information see individual chapters). I was a field assistant to Dr Madden for six weeks in 2000. Although I did not collect data directly for the use of my Ph.D. during this time, it provided me with experience working on spotted bowerbirds, knowledge of the park and the other birds encountered on it.

2.4 Bower description

Spotted bowerbirds are an example of bowerbirds that build avenue-type bowers, along with the other grey (*Chlamydera* spp.), silky (*Sericulus* spp.) and satin bowerbirds (*Ptilonorhynchus violaceus*, Frith & Frith, 2004). The basic bower structure, or avenue, is two parallel walls made of grass and sticks inserted into a platform. A typical spotted bowerbird avenue on Taunton is 450 mm high and 280 mm long. Decorations can be spread several metres away from the avenue (mean distance $\pm$ SD = 1564 $\pm$ 865mm). Over 1000 individual bower decorations are commonly found at a single bower and I recorded a maximum of 1564 (see also Madden, 2001b). The two ends of the avenue are typically decorated with piles of large numbers of white objects, often sun-bleached snail shells or bones. Red and brownish objects are often placed around the edge of the avenue walls. These include red stems, seedpods, "itchy grub cases" (frass formed by beetle larvae boring into the bark of *Acacia* species), as well as artificial objects. Green objects are frequently favoured and displayed in the centre of the avenue; green berries and green glass are especially popular (fig 2.4). One of the most common green decorations, both in terms of absolute numbers and occurrence at different bowers, is the *Solanum* berry (fig 2.5). This berry is medium-sized, green and waxy and is not eaten by the bowerbirds. During my study all bowers had at least one *Solanum* berry at some point, and a maximum of 288 *Solanum* berries were recorded at one bower. The *Solanum* berry is a good predictor of mating success and the males with the most berries gain the most copulations (Madden, 2001b; 2003a).

2.5 Location of bowers

On Taunton, bowers are preferentially situated in areas of brigalow re-growth. Within this habitat males show a preference for building their bowers under bushes bearing edible fruit or those with spines, and those with sufficient space for the avenue and display court (Miles & Madden, 2002). Such bushes include *Heterodendron diversifolium*, *Acacia harpophylla* (brigalow), *Carissa ovata* and *Geijera parviflora* (wilga). There are traditional bower sites where a bower may persist for at least six years (J. R. Madden pers comm., Frith & and Frith, 2004), either in exactly the same place or within an approximate 100m radius. Bowers are regularly spaced within suitable habitats with a nearest-neighbour bower distance of around 1000m (1059 ± 516m: Miles & Madden 2002) although greater distances have been reported for other populations (1830 ± 620m: Borgia & Mueller, 1992). Interference from rival males in the form of bower destruction and stealing of decorations probably maintains the minimum inter-bower distance (Miles & Madden, 2002; Madden et al., 2004).

Bowers were searched for between 28th May and 28th June 2002 and 21st June and 25th July 2003. Initially, I searched for bowers around previous known bower sites, for some of which GPS positions were available (J. R. Madden pers comm.). Once a bower was found it was necessary to determine whether it was currently active. To do this five pieces of labelled glass were placed 2m in front of the avenue and the bower was re-visited three or four days later. Sometimes the glass had been moved onto the bower in which case it was deemed active. On other occasions it had been removed which, after thorough searching of suitable bushes within 100m radius of the old bower, could lead to the discovery of the new, active bower site. Other bowers were located at the beginning of each field season by walking around the field site looking under suitable bushes and following any calls of bowerbirds. Searching was concentrated on areas of brigalow re-growth at least 1000m from known-bower sites. Fifteen active bower sites were found in 2002. In 2003, fourteen of these bowers were still active, two previously known bower sites became active again and five new sites were located, one of which was a practice bower (Frith & Frith, 2004), giving a total of twenty-one active bower sites. I took a GPS position of all bowers and they were plotted on a map of Taunton National Park (see fig 2.6 and A.8).

Fig 2.4: A typical bower on Taunton. Note the red plastic objects to the left of the avenue and green berries and glass in, and in front of, the avenue

Fig 2.5: *Solanum* berries and plant in flower

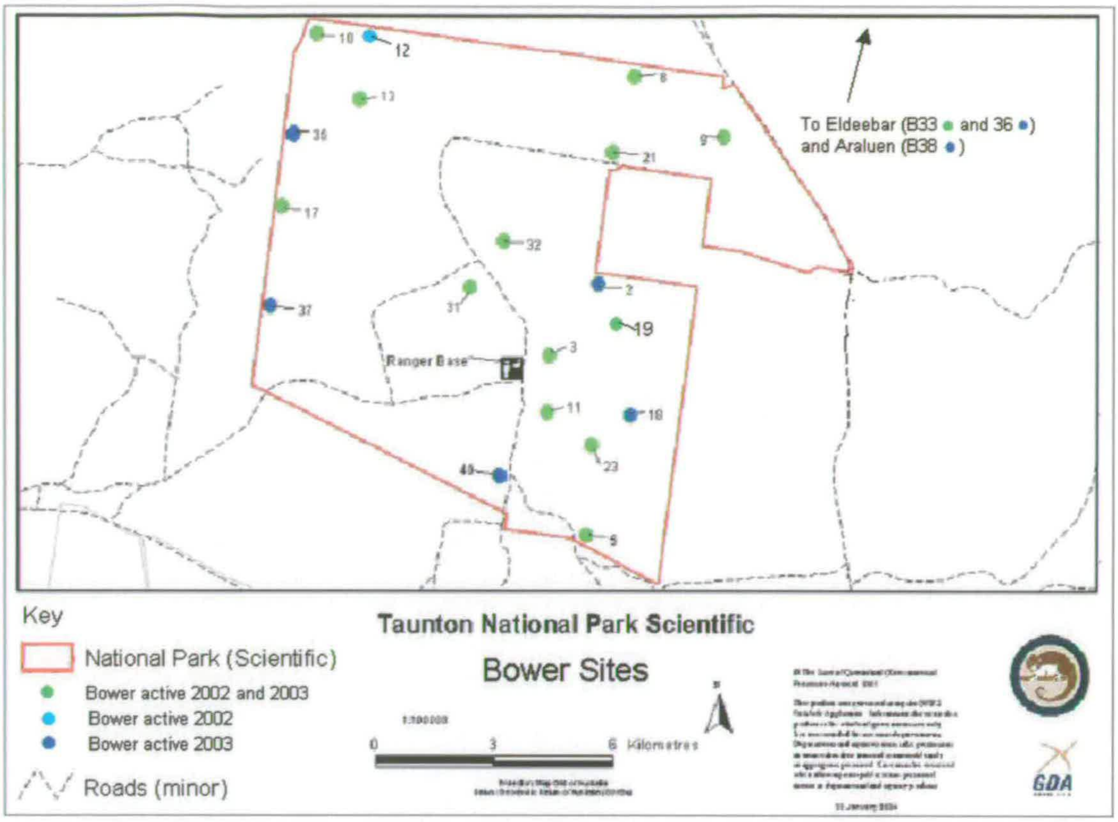


Fig 2.6: Map of bower sites on Taunton National Park

2.6 Capture and banding

In order to identify individual bowerbirds, especially the bower owners, birds were caught and given coloured leg bands. To do this, the ABBBS granted me an R-class banding authority (number 2549) and approval to undertake colour marking. I was unable to obtain this permit until 2003. I caught, and banded, eleven spotted bowerbirds between 1st August and 31st October 2003. The birds were captured using 12m mist nets set up around bower sites or close to popular feeding sites (especially close to introduced fruit trees). Once captured the birds were placed in cotton bags prior to processing. The birds were banded with a metal (size 7) Australian Bird and Bat Banding Scheme (ABBBS) band and a unique combination of five vinyl, coloured leg bands following the schema used by Madden (2001b). The wrap-a-round colour bands were secured using "Selley's PVC glue" (Lowe, 1990). All birds were given the same five colours (red, orange, yellow, dark blue and pale green) to avoid any influence on attractiveness to potential mates (Burley et al., 1982; Burley, 1988). Colour combinations were chosen randomly. 120 bowerbirds had previously been banded with the metal ring and two coloured bands on left leg and three coloured bands on the right (Madden 2001b). The fourteen birds caught subsequently, including the eleven I caught, had the metal ring and two colours on the right and three coloured leg rings on the left.

Fig 2.7: Spotted bowerbird with leg rings (OY-RBG). Note the silver band at the bottom of the left leg.

Whilst handling the birds, basic morphometric measures were also taken. These were mass, bill width and length of tarsus, hind claw, tail, wing and gape (see Lowe 1989). The width and length of the crest was measured as described by Madden (2001b). The colour of the birds' iris, gape and cloacal protrusion were also recorded. These data were submitted to ABBBS but do not form part of the current study.

Spotted bowerbirds are comparatively long-lived (>11-13 years, Frith and Frith 2004) and twelve of the birds banded in 1998 were sighted in 2003. 14 of the 2002 bower owners (see 2.8) and 15 of the 2003 bower owners had been banded between 1998 and 2000. Three birds that were bower owners in 1998 were still owners at the same site in 2003. In total, 21 of the 22 bower owners I studied were banded. Birds caught between 1997 and 2000 were sexed using molecular techniques (Madden 2001b). Only 15 females have been banded and none of these were re-sighted during 2002 or 2003. In addition, 13 auxiliary birds (see 2.8) in 2002 were banded and five in 2003.

2.7 Bowerbird identification

The coloured banding allowed individuals' identities to be ascertained in the field. For ease the birds were known by the first letter of the colour of each of their leg bands read from the top to bottom of the left leg and then the right (see Fig 2.1a and 2.7). Inevitably, it was not always possible to have a clear view of the bands and hence only partial identities were recorded from some sightings. In these situations, if at least three colour bands matched the order and position of a bird previously sighted at the same bower they were assumed to be the same individual, otherwise it was recorded as "ringed". There were still many unringed individuals within the population that could not be individually identified. When a bird's banding status could not be seen the sighting was recorded as "no ID".

2.8 Bower owners and auxiliaries

Bower owners were defined as those individuals who regularly frequented, maintained and displayed at a particular bower and who were in attendance for the greatest proportion of observation time. At all except one bower, the owner was either already banded or was caught and banded in 2003.

Additionally, many bowers at Taunton had an auxiliary male (*sensu* Madden, in prep.). An auxiliary male is usually tolerated by the owner and permitted to perform bower maintenance (bower building or decoration arrangement) and to display in the presence of the owner. I defined auxiliaries as individuals who were present at the bower for more than 10% of the observation time in which one or more bowerbirds were observed. They must also have been witnessed maintaining, displaying, or displacing another bird from the bower. Most of the following data are on the bower owners, but due to their frequent occurrence at bowers, auxiliaries are also included in some of the analyses.

2.9 Bower tenure

Dr Joah Madden studied the same population of bowerbirds at Taunton National Park between 1998 and 2000. Our combined knowledge of ringed individuals was used to assess the duration of bower ownership, or bower tenure. Duration of tenure, was only accurately known for ten individuals during 2002 and 2003. These were individuals that: 1) took over an existing bower between 1998 and 2003, this was assumed to be their first bower 2) were observed to be bower owners for all six years. Six years is considered to be the maximum tenure for spotted bowerbirds (J. R. Madden pers comm.) although this may be an underestimate. There are reports of the same satin bowerbird being an owner for in excess of fifteen years (Frith & Frith, 2004).

The duration of tenure could not be established for the other bower owners because it was not known how long they might have been bower owners before the bower was found. It was also not possible to know whether changes in bower owner between 2000 and 2002 occurred in 2001 or 2002 as no data were collected in 2001. For these owners the *minimum* tenure duration was determined as the number of years since the individual was first observed as a bower owner.

2.10 Observations

Observations at bowers were carried out concurrently with locating new bowers, and commenced on 16th June 2002 and 2nd July 2003. Initial observations were necessary to identify bower owners and auxiliaries (see 2.8). These and subsequent observations in between experiments provided data on the natural occurrence of mimicry. Further information on individual experiments is provided in later chapters, but the following is, unless stated otherwise, common to all of them.

Observations were carried out from between 5:30am and 12:00pm, and 2:00 and 5:00pm, as the birds appeared to be more active at these times (see also Frith & Frith, 2004). In 2002, each of the 15 bowers was visited to conduct an observation or experiment on average every 7.1 days. In 2003, the 20 bowers were monitored every 9.1 days as it was usually only possible to carry out a maximum of three observations per person per day because of the logistic difficulties of moving between bowers. Attendance of bowerbirds at bowers varied considerably throughout the season, overall at least one bird was present for 26% of the total observation time in 2002 (374 hours) and 22% in 2003 (total observation time = 422 hours). Observations lasted between an hour and a half and two hours (see individual experiments for details), although if no bowerbird was sighted within an hour the observation session was terminated.

Initial observations were carried out from behind tarpaulin hides. However, these were quickly discarded as the slightest breeze caused rustling that interfered with the sound recordings, and the observer's field of view was too limited. For all further observations, the observer sat at least 10m from the bower and quietly watched the bowerbirds' behaviour through binoculars. The birds seemed unaffected by the observers and most normal behaviours were observed, including courtship displays and even a forced copulation. In a previous comparison of data collected by human observers and from video recordings from a concealed camera there was no significant differences in the duration and type of activities captured (Madden 2001b).

Observations, experiments and bower locating were carried out with the help of ten field assistants, over the course of the two field seasons. They operated recording equipment and noted the presence and behaviour of bowerbirds and also the timings of all bowerbird vocalisation. Inter-observer reliability is not considered a problem as only I analysed all the recordings, assisted by the field notes. All experiments were carried out with me and a research assistant at the same bower. Our observations were later pooled and showed a high degree of agreement, especially in classification of bowerbird behaviour.

All observations were carried out at the bowers, as these provided a site that known individuals, mainly the bower owners, return to. During the main displaying season (October to November) bower owners spend around 54% of total daylight hours around their bowers, peaking around 8:00am (Frith & Frith, 2004). The identity of all individuals visiting the bower was, where possible, recorded along with its position (at bower, within 10m of bower, 10 – 20m from bower or >20m) and any vocalisations made, and the time (taken from the Sony DAT recorder counter (see below) or a stop watch. Bowerbird behaviour was recorded according to the definitions of Madden (2001b) as follows:

Maintaining bower – bird tends to the avenue walls or adds or moves decorations.

Display – bird performs typical, vigorous display movements (including wing flicks, leaps, crest presentations and picking up and tossing decorations, all accompanied by continuous hissing vocalisations) in the presence of another conspecific

Practice display – bird performs typical display movements as above but in the absence of a conspecific

Destroying – bird wrenches the avenue platform apart with its bill in a series of violent tugs and jumps

Supplanting – bird charges at second conspecific repeatedly, until it leaves the bower area

Additionally, preening, feeding and decoration-stealing behaviour were recorded. Every five minutes of an observation a one-minute census of heterospecifics seen and heard around the bower was carried out. This included any birds that could be visually identified from within around 30m, as well as any birds, including raptors, spotted flying overhead.

2.11 Recording techniques and equipment

Most recordings were made using a Sony TCD-D8 DAT recorder and an Audio Technica AT 822 microphone. The DAT recorder remained at the side of the observer for ease of manipulation and accurate recording of times of vocalisations from the counter. The microphone lead was extended fully towards the bower. In 2003 a Sony Walkman Mz-NZ10 mini disc player and a Sony ECM-MS907 microphone were also used to record vocalisations. This mini disc player combined with Sony SRS-T55 speakers were used in the playback experiment (see 4.4).

2.12 Bowerbird calls and mimicry

Spotted bowerbird calls mainly consist of harsh grating hisses and quieter "mechanical noises" (Simpson & Day, 1999). The hisses tend to become more screechy and continuous during displays. The birds also make a distinctive "advertisement" call which consists of two to four short, sharp hisses often delivered from a vantage point on top of a tree (Westcott & Kroon, 2002; Frith & Frith, 2004). The function of these calls is presumed to be to advertise the location of the bower and the attendance of the bower owner to potential mates and possibly rival males. In addition, bowerbirds were heard to mimic 14 avian models, as well as cat-like calls (which may or may not be mimetic see 1.2) and mimicry of dogs. The avian models are listed in table 2.1. There are also some calls that may have been mimicry of models I was unable to recognise. For examples of spectrograms see fig 2.9 and A.1.

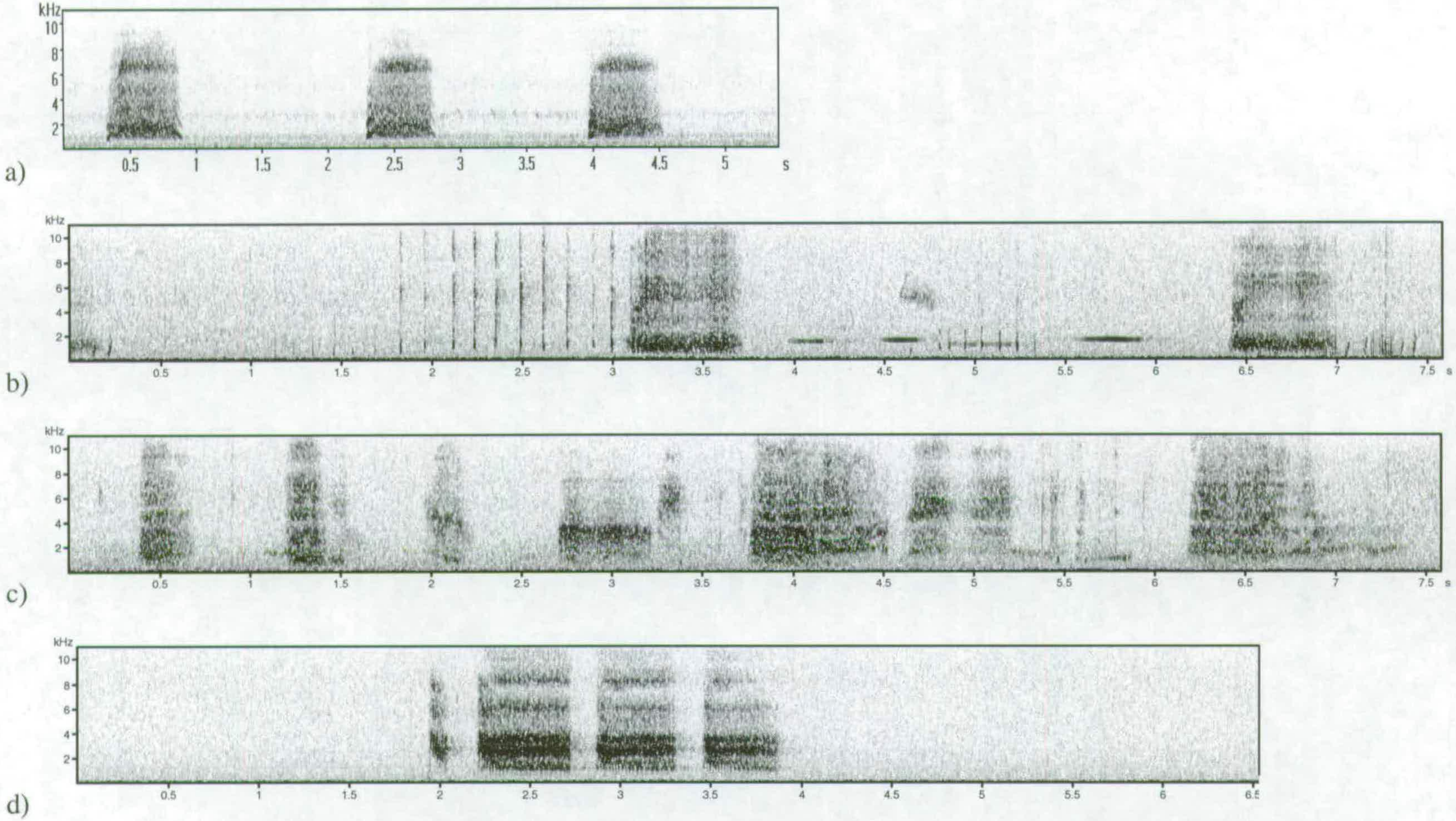
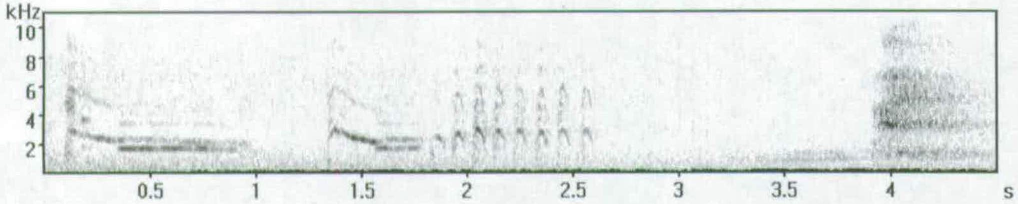


Fig 2.8: Spectrograms showing examples of species-specific calls **a)** hiss at rest **b)** mechanical noises – bill clicks at 2sec and 4.8 plus hiss **c)** display hiss and **d)** advertisement call (see 2.13 for details of settings).

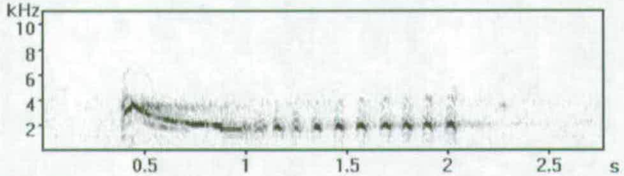
2.13 Analysing sound recordings

The rate of species-specific hisses was calculated by converting recordings to spectrograms like those in figure 2.8, created using Avisoft SAS LabLight (version 3.74, R. Specht, 1999), and counting the number of distinct bands, each of which correspond to an individual hiss. All spectrograms presented use the standard settings available on this version of Avisoft (FFT length = 256, frame size = 100%, window = Hamming, overlap between frames = 50%).

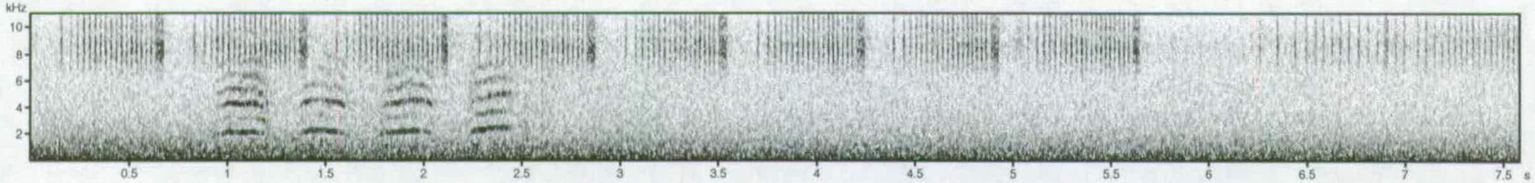
Mimicry was recognised by listening to recordings, assisted by visual representation on spectrograms produced in Avisoft. Calculating the rate of mimetic calls (for definition see section 1.1, Baylis, 1982) was not as obvious as for the species-specific calls, as they do not conform to easily identifiable elements like the hiss. One unit of mimicry was hence defined as the smallest element that could be recognised as mimicry of that particular model species. This may cause mimicry of calls of birds like the noisy miner or the babbler to give an artificially high rate of mimicry as the calls consist of highly repetitive syllables (see fig 2.9, Catchpole & Slater, 1995).



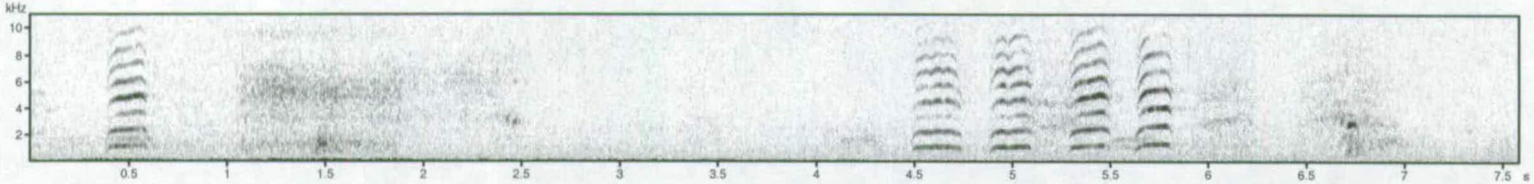
a) Mimicry of whistling kite– note species-specific hiss at 4 seconds. This would represent 2 units of mimicry as the first descending whistle (0.1 to 1 sec) is recognisable on its own but the staccato "si-si-si-si" elements (1.7 to 2.6s, Simpson & Day, 1999) of the second call are only recognisable when preceded by the whistle.



b) Whistling kite model



c) Noisy miner mimicry. There are 4 mimetic units in this example of mimicry, each of which is a very similar syllable (NB sounds between 8 and 10kHz are cicada calls).



d) Noisy miner model

Fig 2.9: a-d Examples of models and mimics (see 2.13 for details of spectrogram settings)

Common names	Latin names
Apostlebird	*Struthidea cinerea*
Australian magpie	*Gymnorhina tibicen*
Brown falcon	*Falco berigora*
Bush stone curlew	*Burhinus grallarius*
Butcherbird	*Cracticus* spp.
Fairy wren spp.	*Malurus* spp.
Grey-crowned babbler	*Pomatostomus temporalis*
Laughing kookaburra	*Dacelo novaeguineae*
Noisy friarbird	*Philemon citreogularis*
Noisy miner	*Manorina melanophrys*
Red winged parrot	*Aprosmictus erythropterus*
Torresian crow	*Corvus orru*
Whistling kite	*Haliastur sphenurus*
Willie wagtail	*Rhipidura rufifrons*

Table 2.1: Avian species mimicked by spotted bowerbird

When more than one bowerbird was present it was not always possible to determine which bird was vocalising because they move very swiftly around the bower, frequently swapping position or going out of sight for short periods. Even if it was possible to recognise when each individual was vocalising in the field, it was not possible to transcribe all events so that calls could be accurately attributed to each individual during subsequent sound analysis. It was therefore necessary to make one of two assumptions when calculating rates of vocalisation:

1) assume that all calls are made by the bower owner
2) assume that calls are shared equally amongst the bowerbirds present.

The first assumption may be more realistic as the bower owner was generally more vocal relative to visiting conspecifics. The data produced as a result of each assumption were analysed separately. Unless stated otherwise, the data are from solitary bower owners only.

2.14 Reliability of visual spectrogram classification

Many studies, including my own, use visual inspection of spectrograms to answer questions about vocalisation (e.g. Feekes, 1982; Cruickshank et al., 1993; Kaplan, 1999; Jones et al., 2001). For instance, comparison of spectrograms can be used to determine whether a juvenile has learnt its songs from a certain tutor or, as in this case, whether a species is mimicking a particular heterospecific. However, this classification can be largely subjective and may depend on how the observer weighs different aspects of a spectrogram. This can be biologically significant. For instance, a human observer may give equal emphasis to the frequency and duration of a sound although psychophysical experiments have shown that birds are much more sensitive to changes in frequency than duration (Dooling, 1982). Despite the obvious difficulties in categorizing spectrograms, few studies offer figures of inter-observer repeatability or reliability (Jones et al., 2001).

I classified all of the vocalisations myself by visual inspection of spectrograms, often confirmed by listening to the call recordings. However, to check both the generality of my classificatory decisions and the subjectivity of this method, I carried out a small investigation into its reliability. In particular, I aimed to see if volunteers matched spotted bowerbird mimicry with the same heterospecific models as I did.

Method

Five types of bowerbird mimicry were selected on the basis that 1) they occurred in the recordings of at least three birds, 2) I had at least ten examples of the mimicry recorded on spectrograms and 3) I had a suitable spectrogram of the model species vocalisation. The five types chosen were whistling kite (*Haliastur sphenurus*), grey-crowned babbler (*Pomatostomus temporalis*), apostlebird (*Struthidea cinera*), noisy miner (*Manorina melanocephala*) and Australian magpie (*Gymnorhina tibicen*). For each of these, I chose an example of the model species vocalisation that I considered to be a good match for the mimicked calls.

A set of thirty-five test spectrograms was compiled (for examples, see A.1), each spectrogram displaying 7.5 seconds. These consisted of five spectrograms of bowerbirds mimicking each of the five model species above, five spectrograms of bowerbird mimicry of other model species plus five spectrograms believed to be mimetic but of unknown models. The spectrograms were chosen at random from each of these categories. The order of the spectrograms was randomised and they were printed out three per page. If other sounds (i.e. heterospecific calls, other bowerbird vocalisation or environmental noises) were visible on the spectrogram, arrows pointed to the relevant call or calls.

Tests were carried out between 12th and 15th April 2005, using six volunteers from the University of St Andrews. These individuals all had previous experience analysing spectrograms, although the range and type of experience varied. Some usually worked on bird song while others usually analysed sounds produced by cetaceans. They were all given the same written instructions with only minimal verbal clarification. Volunteers were given two sets of spectrograms. The first was the thirty-five spectrograms of bowerbird mimicry. The second was a set of six example spectrograms, one of each of the five model species' calls and also one of the grey fantail (*Rhipidura fuliginosa*). The fantail was one of the birds heard most frequently at the bower but was never mimicked by the bowerbirds. The volunteers were asked to match the first set of spectrograms to the six categories represented by the example spectrograms or to an additional, seventh category, "none of the above".

Volunteers were not told the species of the example calls, nor how many of each type of call to expect. The order of presentation was changed among volunteers by shuffling the pages to help control for any order effect. After completing the task, the subjects were invited to give feedback on it, including any comments as to how they came to their decisions.

The responses of each volunteer were compared to the "correct" categorisation (i.e. my categorisation of the same calls) of the spectrograms and the proportion of agreement was calculated. The Kappa coefficient (Martin & Bateson, 1993; Jones et al. 2001) was also calculated for each observer allowing a measure of the observed agreement between us against the expected agreement by chance. Whilst it is possible to adapt the Kappa coefficient for more than one observer, here I was more interested in how well each observer agreed with my categorisation rather than agreement among themselves.

The Kappa coefficient is calculated from the following formula:

$$\kappa = (O-C)/(1-C)$$

where O is the observed proportion of agreements and C is the proportion of agreements expected by chance. The proportion of spectrograms that I categorised as belonging to group A is multiplied by the proportion of spectrograms observer 1 placed in the same category. This is repeated for all seven categories and the products summed to give the value for C. Hence, for observer 1:

	my categories	observer 1
A	5	5
B	5	6
C	0	1
D	5	5
E	5	6
F	5	7
G	10	5
Proportion agreement:		28/35=0.8

Table 2.2: summary of observer 1's categorisation of the spectrograms

$C = (5/35 \times 5/35) + (5/35 \times 6/35) + (0/35 \times 1/35) + (5/35 \times 5/35) + (5/35 \times 6/35) + (5/35 \times 7/35) + (10/35 \times 5/35)$

$C = 0.159$

$\kappa = (0.80-0.159)/(1-0.159)$

$\kappa = 0.762$

This is then repeated for each individual observer. The closer the value of κ is to 1.0, the more the observed degree of matching deviates from chance, i.e. the higher the inter-observer reliability. A value of zero indicates the matching is no better than expected by chance and negative values indicate less matching than would be expected by chance. The strength of agreement between observer 1 and me is therefore good.

Results

The mean proportion agreement and the kappa coefficient show a reasonable degree of agreement between six observers and me (table 2.3). All of the Kappa coefficients show a greater degree of matching than would be expected by chance alone. However, there is variation in the extent of agreement among the observers. In particular, observer 5 scores a fairly low Kappa coefficient value. Closer inspection revealed that observer 5 categorised many of the spectrograms as category G, "none of the above" (see table 2.4). Observer 5 explained at the time of the test that he was used to looking at very small differences in vocalisations and applied a very stringent criterion for the matching of mimetic calls to their proposed models. In particular, he paid close attention to the formant structures and did not rank model and mimic as matching if the highest energy formants did not match.

Observer:	1	2	3	4	5	6	mean
Proportion agreement	0.800	0.771	0.771	0.600	0.514	0.857	0.719
Kappa coefficient	0.762	0.708	0.713	0.487	0.360	0.826	0.643

Table 2.3: Summary of inter-observer reliability measures when compared to my categorisation

			Number categorised by observer:						
Category		**% matching**	**me**	**1**	**2**	**3**	**4**	**5**	**6**
apostlebirds	**A**	54.29	5	5	4	4	2	0	5
babblers	**B**	62.86	5	6	1	5	4	4	6
grey fantail	**C**	na	0	1	0	0	0	0	0
whistling kite	**D**	54.29	5	5	4	3	4	0	5
magpie	**E**	68.57	5	6	4	5	4	5	6
noisy miner	**F**	48.57	5	7	4	3	2	2	4
none of above	**G**	78.33	10	5	18	15	19	24	9

Table 2.4: Summary of the scores observed for each category of spectrogram

The matching of my and observers' categories was much higher for some spectrograms than others. However, there did not appear to be one category that was much more difficult to classify correctly than any of the others (table 2.4). The greatest percentage matching was observed for the "none of the above" category (G). This also accounts for the Kappa coefficient values being lower than the proportion matching values. The Kappa coefficient takes into account the degree of matching by chance, which would be relatively high if the observer had classified many spectrograms in category G. Hence, observer 5's especially low Kappa coefficient. Most non-matching occurred because calls I had identified as mimetic were placed in category G. On only 19 occasions did an observer categorise a spectrogram as a different type of mimicry (9.0% of all classification decisions).

Discussion

Overall, the inter-observer reliability tests revealed a reasonable level of agreement between my classification and that of the six volunteer observers. It is noteworthy that a lack of agreement usually occurred because a spectrogram was categorised as "none of the above". Only on a few occasions were spectrograms placed in the category of a different model. Therefore, whilst these other assessors may have recorded a lower rate of mimicry, they seem to have agreed with me on the types of mimicry recorded. I, therefore, feel that I can be reasonably confident in my assessment of mimetic vocalisations and that other observers would draw broadly similar conclusions from the same data.

Some calls were identified "correctly" more often than others. After the investigation I looked at the spectrograms that were most frequently misidentified. Unsurprisingly, these were spectrograms where the call was very faint or was obscured by background noise or other calls. It was useful to include these spectrograms in the random selection of test spectrograms to highlight some of the difficulties encountered when identifying bird song from the less-than-perfect recording conditions experienced in the field. Some of these calls may have been easier to identify by listening to them.

It is clear that my criteria for classifying mimicry as matching a model were not as strict as those used by some other observers (in particular observer 5) which may possibly have caused me to over-estimate the occurrence of mimicry. However, I was not entirely reliant on the visual classification of calls and would listen to them as well. Ideally, the volunteer observers would have been provided with the same access to visual and aural representation of the mimicry as I had when originally classifying the calls.

There are further limitations of this investigation into inter-observer reliability. I attempted to make the investigation as fair as possible by including mimetic types that did not belong to any of the model categories and a potential model that was not mimicked, but the answers of the volunteers were limited to the seven categories chosen by me. When I classified the mimetic calls I was guided by previous observations (Warham 1962, J. R. Madden pers comm.) as to likely models of spotted bowerbirds, but could add new categories of mimicry if necessary. However, it would not be feasible to set up an inter-observer reliability test with the spectrograms of all possible models. There was also an issue of pseudoreplication (McGregor, 2000) as the model calls were only represented by one spectrogram. Whilst I could have selected several model spectrograms at random as I did for the mimicry, this would have made the test more complicated and time consuming for the volunteer observers.

This investigation highlighted some of the difficulties encountered in categorizing types of mimicry by visual inspection alone. It is not ideal to have just one person categorizing a type of behaviour or, as in this case, a type of call without some external check (Martin & Bateson, 1993; Jones et al., 2001). However, in this study, it was not feasible for an extra observer to score even a subset of the recordings, due to time constraints. This inter-observer reliability test, despite its limitations, was relatively successful in assessing the generality of my classification decisions. It allows a degree of confidence in my analyses as it showed that others can repeat the classification of spectrograms with a reasonable amount of agreement.

2.15 General statistical methods

Unless stated otherwise, all statistical analyses were carried out on Minitab (Release 13.0, Minitab Inc., State College, PA). When constructing General Linear Models (GLM), the assumptions of normality were tested with Kolomogorov-Smirnov test and the homogeneity of variance with Bartlett's (normally distributed data) and Levene's (non-normal, continuous data) tests. Where necessary data were transformed to meet the assumptions of parametric tests. Time, where appropriate, was entered as a linear co-variate. All tests were two tailed.

Repeated measures of vocalisation rate were taken on each bowerbird. However there were missing data points such that data were not available for all individuals under all conditions (e.g. presence and absence of competitors). This meant the interaction term of the full model (i.e. rate = individual + treatment + treatment*individual) could not be tested using all individuals. Inspection of the subset of individuals for which data were available under all conditions revealed that in many cases the interaction was a significant term: different individuals reacted to the various conditions in different ways. In most cases the difference was in the magnitude of the change in vocalisation, with the trend being in the same direction across individuals, however, there were also a few individuals which either showed no change in vocalisation rate in the different conditions or seemed to change rate in the opposite direction to the majority. Individual differences such as these are considered in more detail in chapter 5. As it was not possible to test the treatment term over the interaction term nor to assume the interaction was zero, for the purposes of chapter 3 and 4 the issue of repeated measures within individuals was addressed by taking a mean vocalisation rate for each individual in each condition and testing this in the GLM (rate = individual + condition).

Another assumption of testing repeated measures data that should be met is one of sphericity: i.e. the assumption that there are no correlations among treatments not caused by the treatment effects themselves. This is only an issue for experiments with two or more treatments and so does not affect the analyses of chapter 3. The assumption is likely to be met if treatments are applied at random to different individuals on different days (as in section 4.2, Quinn & Keough, 2002). However, the assumption is more likely to be violated in section 4.3 where vocalisation rates before, during and after a disturbance event are compared. Due to the temporal nature of this study the rate before is more likely to be correlated with the rate during than the rate recorded after, hence there is likely to be a relationship among the rates at subsequent stages that is not due to just the treatments alone. A comparison of the variances of differences between treatments can act as an indicator of violation of the assumption of sphericity (Quinn & Keough, 2002). I was unable to detect a significant difference between the largest and smallest variance of differences in section 4.3 ($F_{9,9} = 2.4$, $p>0.05$) so, therefore, am reassured the assumption was not violated. However, I am aware that there are alternative multivariate analyses that do not make this assumption of sphericity, which would be more appropriate for the analysis of this experiment prior to publication.

2.16 Ethics approval

I was granted ethical approval for this study by the University of Queensland Animal Ethics Committee (ZOO/ENT/039/02/NERC/PhD & ZOO/ENT/194/03/NERC/PhD). In addition, I had Queensland Parks and Wildlife Services permits (see 2.2) and banding authority from the Australian Bird and Bat Banding Scheme (see2.6).

Chapter 3. Why do spotted bowerbirds mimic? Observational data

3.1 Introduction

The function of mimicry is poorly understood (Dobkin, 1979, see also chapter 1). Whilst many studies have observed the occurrence of mimicry, far fewer have actually attempted to quantify which models are mimicked and when mimicry occurs (Hindmarsh, 1984; 1986; Chu, 2001b). Quantification of what is mimicked and when, under natural conditions, might provide an indication as to its function.

Analysis of which models are mimicked has not yet provided good evidence that predators or competitors are preferentially mimicked, as is predicted from the Beau Geste or the Batesian acoustic mimicry hypotheses (Howard, 1974; Hindmarsh, 1984; Chu, 2001b; Chu, 2001a; Ferguson et al., 2002; Hamao & Eda-Fujiwara, 2004). Phainopeplas (*Phainopepla nitens*) are observed to mimic predator-mobbing heterospecifics, as would be expected if mimicry caused the intervention of a third species. However, the model species were more likely to mob in response to the phainopeplas species-specific alarm call than the mimicry of their own calls (Chu, 2001a). This shows that analysis of which models are mimicked is not sufficient on its own and hypotheses should also be tested experimentally.

There is mixed support for the prediction from the Learning Mistakes hypothesis that common calls should be preferentially mimicked. Phainopeplas and robin chats (*Cossypha* spp.) do not mimic the calls most commonly heard in the sound environment (Chu, 2001b; Ferguson et al., 2002) whilst European starlings (*Sturnus vulgaris,* Hindmarsh, 1986) and black-browed reed warblers (*Acrocephalus bistrigiceps*, Hamao & Eda-Fujiwara, 2004) do. However, it is possible that the calls of some of the common species in these studies were beyond the vocal capabilities of the mimic (Kaplan, 1999; Podos, 2001). Model calls that are mistakenly learned should also be relatively simple and similar to the mimic's own calls. Again, the evidence is mixed: for example, Hindmarsh (1986) found that starlings did show a preference for mimicking calls with a simple structure and clear notes, although did not comment as to whether these calls were similar to the starling species-specific calls. By contrast, the mimicked calls of the Australian magpie (*Gymnorhina tibicen*) include many formants and modulations lacking in the pure notes of its species-specific vocalisation (Kaplan, 1999), suggesting mistakes made during song learning do not cause the mimicry observed in this species.

It is less obvious what type of models would be mimicked if the function of mimicry was social affiliation, either in the form of phatic communication (Robinson, 1991) or individual recognition (Harcus, 1977). Robinson suggested that the lyrebirds (*Menura* spp.) use mimicry to maintain contact with conspecifics without conveying any particular signal of threat, alarm or reproductive status. He found that the lyrebirds tend to mimic calls outside of the breeding season of the model species when, he claimed, the calls were also of no biological significance to the models (Robinson, 1974). Differences among individual conspecifics' mimetic repertoires need to be studied for evidence of individual recognition (see 5.3), for instance to see if neighbours actively avoid mimicking the same or similar calls to facilitate recognition (Hausberger et al., 1991). Affiliative call convergence might be limited to copying conspecific calls (Vehrencamp et al., 2003), but perhaps the ability to copy subtle differences in species-specific calls offers a mechanism by which heterospecific mimicry can occur (Cruickshank et al., 1993).

Sexual selection might drive a tendency to increase the size of the mimetic repertoire (e.g. Hiebert et al., 1989) or the quality of mimicry (Loffredo & Borgia, 1986). Using mimicry simply to increase the repertoire size does not lead to specific predictions as to which models should be mimicked. However, it is conceivable that complex calls that are difficult to mimic might be good indicators of male quality and therefore favoured by sexual selection (Gibson & Bradbury, 1985; Gil & Gahr, 2002; Slater, 2003). There may also be a tendency for females to show a preference for mimicry of novel songs (ten Cate & Bateson, 1988), although again novelty in itself does not lead to predictions about the type of model to be mimicked.

Using the rate and occurrence of vocal mimicry throughout a season to understand the function of mimicry is even more difficult as there are so few relevant data. Fergusson et al. (2002) showed that different species of robin chats (*Cossypha* spp.) mimicked at different rates but there was no discussion of a link between this and the function of mimicry in these species. If mimicry is involved in sexual selection the rate of mimetic vocalisation might be expected to increase during the breeding season and in the presence of conspecifics (as in species-specific song: Eens et al., 1993). Although Loffredo and Borgia (1986) found that males that sang the longest bouts of mimicry had the highest mating success, no one has looked at whether the rate of mimicry changes within or outside the mating season (e.g. Robinson, 1974; Loffredo & Borgia, 1986; Frith & Frith, 1993). Evidence is also lacking for increased mimicry in the presence of predators and competitors as might be predicted by the Batesian mimicry (Dobkin, 1979) and Beau Geste hypotheses (Rechten, 1978). If mimicry were important in individual recognition (Harcus, 1977), an increase in rate in the presence of conspecifics might be expected but this also remains untested. Mimetic vocalisation might be randomly inserted into, and used under the same conditions as species-specific vocalisation if mimicry is a result of mistakes during learning (Hindmarsh, 1986). If this were the case rates of species-specific and mimetic vocalisation would be positively correlated.

In this chapter, I use data from observations of the bowerbirds and other birds around the bower to test whether there is a tendency to mimic particular types of models. I look at the rate of mimicry in the presence of heterospecifics, both competitors and aggressive species, and also in the presence of conspecifics. I consider whether the rate of mimicry changes over the course of the field season. Due to the lack of predictable seasonality in the field site, I also look at the influence of rainfall on the rate of mimicry as it is thought to be an important cue for the commencement of mating in the spotted bowerbird (Madden, 2001b). I also examine how the rate of *species-specific* vocalisation changes in the presence of other birds and throughout the season. Finally, I look for a correlation between the rates of species-specific vocalisation and mimetic vocalisation.

3.2 Methods

Spotted bowerbird models

Between 4th July and 14th August 2002, 47 observations were carried out at 14 bowers. Observations were carried out between 6:00am and 12:00pm and between 2:00 and 5:00pm. Each observation period lasted 120 minutes. For one minute out of every five, I noted all heterospecific birds heard or seen in the surrounding area (up to approximately 30m from the bower). I also recorded all vocalisations made by the bowerbirds, including which species were mimicked.

To test whether competitor birds were preferentially mimicked, the 40 most commonly heard birds at the bower were classified as competitors or non-competitors of bowerbirds according to their feeding habits. Spotted bowerbirds are mainly frugivores, although they do occasionally supplement their diet with invertebrates (Frith & Frith, 2004), therefore any species whose main source of food is berries and fruit was classified as a competitor. Two independent ornithologists with knowledge of the birds found in the field site were also asked to assign the birds to these categories (see A.2). Due to the subjective nature of the definition, discrepancies occurred in the classification of 14 of the 40 species observed. To allow for these discrepancies, the following assumptions were tested in the analyses:

a) Conservative assumption: if disagreement occurred over a species, it was assigned to the non-competitive category

b) Extreme assumption: if disagreement occurred over a species, it was assigned to the competitive category

Similarly, to test whether aggressive species were preferentially mimicked, the 40 most commonly heard birds were assigned to the categories of aggressive and non-aggressive. Aggressive birds were defined as those that are predatory or that commonly displace other birds by threatening vocalisation or mobbing behaviour. They also included birds that have been observed to destroy bowers. Independent confirmation of these categories was sought (see A.3). There was, again, difference of opinion in 3 out of 40 species classified, and the following assumptions were tested:

a) Conservative assumption: if disagreement occurred over a species, it was assigned to the non-aggressive category

b) Extreme assumption: if disagreement occurred over a species, it was assigned to the aggressive category

To test whether commonly heard birds were mimicked more frequently, I divided all of the heterospecific birds heard during observations into commonly or rarely heard categories (see A.4). Commonly heard birds were defined as those which were heard more frequently than the median value (i.e. more than 12 times during the observations) whilst rarely heard were those heard less often than this.

I also looked to see whether mimicked calls were simple and similar in structure to species-specific calls. Some calls mimicked by the spotted bowerbird may be deemed simple to the human auditory system, for instance, the call of the noisy miner (*Manorina melanocephala*) is a series of highly repetitive squawks (see fig 3.1a) while others appear to be more complex, for example, the whistling kite (*Haliastur spherurus*, fig 3.1b). Neither the noisy miner nor the whistling kite mimicry sound or look similar to the species-specific hiss (fig 3.1d), whereas the mimicry of the apostlebird (*Struthidea cinera*, fig 3.1c) is a harsh, grating sound with a similar structure.

To assess whether bowerbirds preferentially mimic calls that are simple or similar to their own calls, spectrograms of both mimicked and non-mimicked birds were scored for their complexity (*sensu* Hindmarsh, 1984). A total of 39 spectrograms were rated, chosen for their availability on my or professional recordings (Simpson & Day, Birds of Australia 5.0). 16 of these spectrograms were of calls mimicked by bowerbirds and 23 were of calls of other heterospecifics observed around the bower. The complexity of each call was scored for three categories listed below, where the higher scores represent increased complexity (for further details see Hindmarsh, 1984). The scores given to the four example spectrograms shown in fig 3.1 are given in table 3.1.

a) Frequency structure
1 = single frequency
2 = most energy in 2 or 3 frequencies
3 = multiple but discrete frequencies
4 = no clear division into frequencies

b) Amplitude modulation
1 = single pure note
2 = single unclear note
3 = several pure notes
4 = several unclear notes
5 = many pure notes
6 = many unclear notes

c) Frequency modulation
1 = none
2 = single modulation
3 = simple
4 = complex

	Frequency structure	Amplitude modulation	Frequency modulation
Noisy miner	3	5	2
Whistling kite	2	3	3
Apostlebird	4	2	1
Species-specific hiss	4	2	1

Table 3.1: Complexity scores for four exemplar spectrograms: three mimicked species and the species-specific hiss (see Figure 3.1)

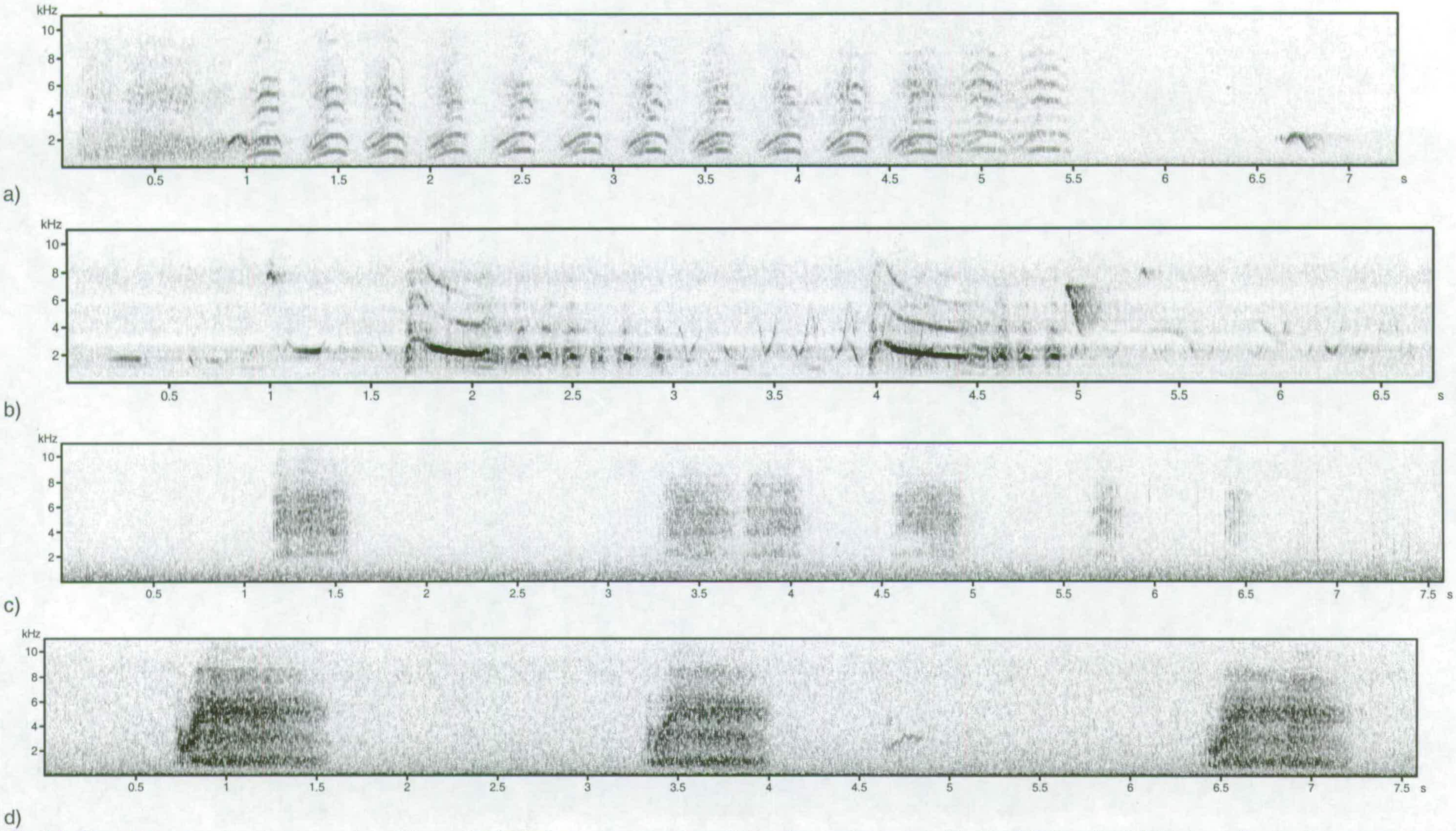


Fig 3.1: Spectrograms showing examples of bowerbird mimicry: a) noisy miner (*Manorina melanocephala*); b) whistling kite (*Haliastur spherurus*); c) apostlebird (*Struthidea cinera*) and d) spotted bowerbird species-specific hiss (see 2.13 for details of spectrogram settings).

The occurrence of mimetic and species-specific vocalisation

Between 16th June and 3rd September 2002 and 2nd July and 26th November 2003, 263 hours and 353 hours, respectively, of observations were carried out. During this time the behaviour and vocalisation of bowerbirds were recorded as described previously (see 2.10). The number of mimetic calls were counted and identified (see section 2.13 and 2.15) and an average rate of mimicry per ringed bird was calculated. The same was calculated for species-specific vocalisation. The presence and identity of heterospecifics within 30m of the bower, including those overhead, were also noted. When more than one bowerbird was present it was not always possible to accurately attribute the vocalisation to the correct bird, therefore two assumptions were tested 1) all vocalisation was attributed to the bower owner and 2) vocalisation was shared equally among the bowerbirds present (see 2.13).

Rainfall data were collected every day for Taunton National Park by Queensland Parks and Wildlife Services rangers, except for a short period when no ranger was on duty. Missing data were provided by the Bureau of Meteorology, collected every day in the nearby Dingo Post Office (23.6450 S, 14.3330 E).

Statistical analyses

χ^2 contingency tables were used to test whether the bowerbirds preferentially mimicked common, aggressive or competitor species or calls that were simple or similar to species-specific hiss. A Mann Whitney U test was used to test for differences between mimicked and non-mimicked calls.

Whilst all analyses were performed for both extreme and conservative assumptions (i.e. of competitive and aggressive species) in all cases the results are qualitatively the same. Thus I present only results under the extreme assumption (b).

Lists of the species belonging to each category can be found in the appendix (A.2 to A.4). The occurrence or absence of mimicry by each bird during each observation gave a binomial distribution that was analysed using logistic regression and mixed effects model in S-Plus (version 6.0; Insightful Inc.). Insufficient data prevented the testing of interactions in General Linear Models (e.g. between individual and the condition e.g. presence/ absence of competitor), these are assumed to be zero.

3.3 Results

Spotted bowerbird models

Mimicry of competitors

Bowerbirds did not mimic a greater proportion of competitor species than non-competitor species (χ^2 2x2: d.f. =1, $\chi^2 = 0.860$, n=40, p=0.354, fig 3.2).

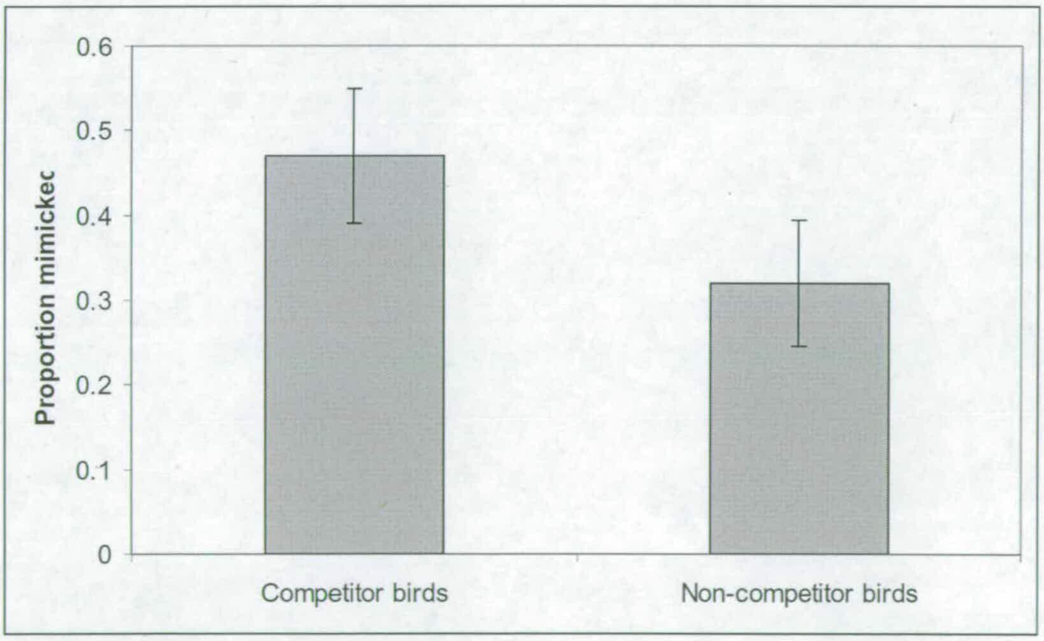


Fig 3.2: Proportion of competitor (7 out of 15) and non-competitor (8 out of 25) birds mimicked by bowerbirds (±SD of binomial distribution, see Sokal & Rohlf, 1969) (using the extreme assumption (b). See A.2 for list of competitor and non-competitor species.)

Mimicry of aggressive species

Aggressive species were more likely to be mimicked than non-aggressive species (χ^2 2x2: d.f. =1, χ^2 =12.715, n=40, $p<0.001$, see fig 3.3).

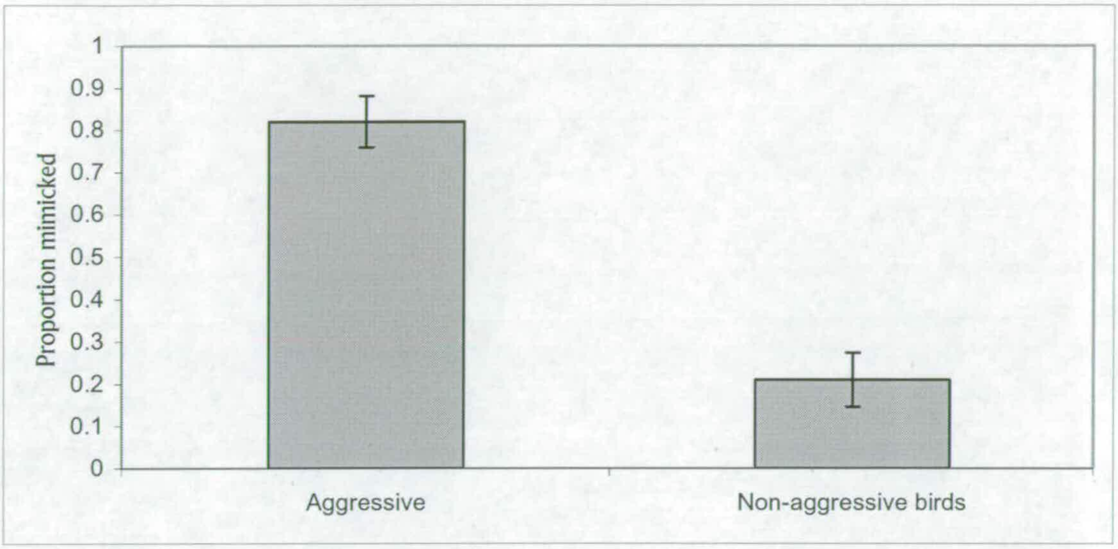


Fig 3.3: Proportion of aggressive (9 out of 11) and non-aggressive (6 out of 29) birds mimicked by bowerbirds (±SD of binomial distribution, using extreme assumption b). See A.3 for list of aggressive and non-aggressive species).

Not all of the birds mimicked were aggressive, although a majority were. To test whether the remaining models tend to be common (see below) or competitor birds, the aggressive birds were removed to prevent them masking any trend and the χ^2 analyses repeated. There was still no tendency to preferentially mimic competitor or common birds; this was true of all combinations of assumptions (χ^2 2x2: χ^2 = 0.806 –1.453, d.f. = 1, n=32, p=0.228 – 0.660).

Mimicry of common calls

51 bird species were heard around the bower, of these 13 were mimicked by the bowerbirds. There was no tendency to preferentially mimic rare or commonly heard birds (χ^2 2x2: χ^2 =1.695, d.f. =1, p=0.193, see fig 3.4).

Fig 3.4: Histogram of proportion of commonly (6 out of 26) and rarely heard (10 out of 25) birds that are mimicked by bowerbirds (±SD, n = 51, i.e. total number of birds heard, see appendix A.4 for list of common and rare species)

Mimicry of simple calls

There were no differences between the structure of mimicked and non-mimicked calls in any of the measures of call structure (Mann Whitney U-test: W = 258 – 371, $n_1 = 16$, $n_2 = 23$, p=0.10 –0.69). There was also no tendency for bowerbirds to mimic more simple (or more complex) calls (frequency structure: $\chi^2 = 4.68$, d.f. = 3, p= 0.20; amplitude modulation: $\chi^2 = 5.86$, d.f. = 5, p = 0.321; frequency modulation: $\chi^2 = 3.34$. d.f. = 3, p = 0.34, see fig 3.5).

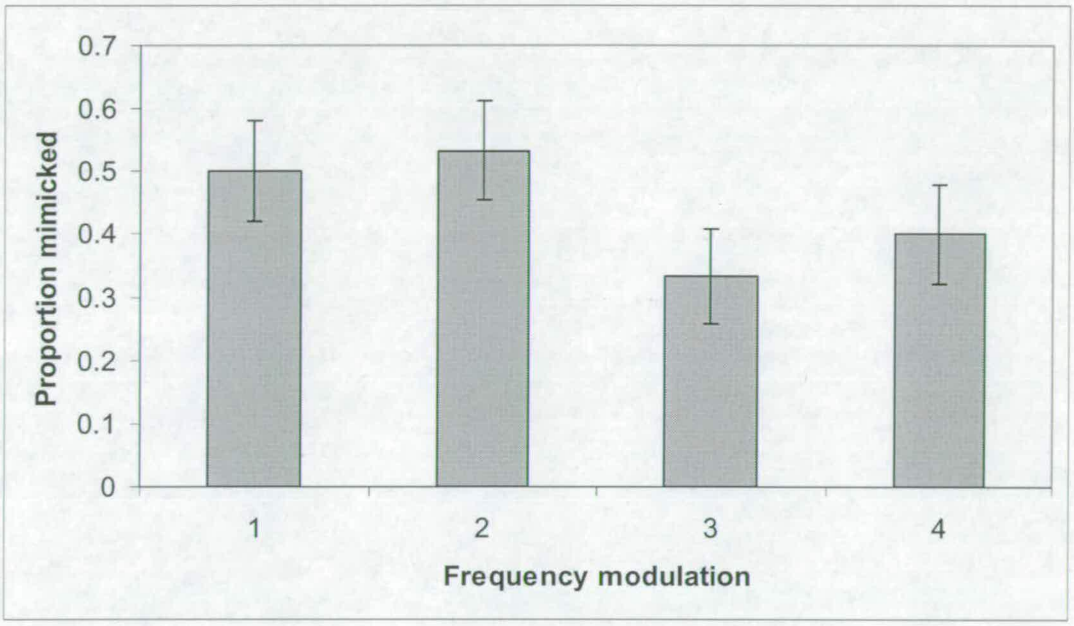


Fig 3.5: Proportion of calls of each category of frequency modulation mimicked by bowerbirds (± SE, frequency modulation 1, n=8; 2, n=15; 3, n=9; 4, n=10)

Mimicry of similar calls

The calls mimicked by bowerbirds did not have the same frequency structure or frequency modulation as the bowerbird's species-specific hiss (frequency structure: $\chi^2 = 2.17$, d.f. = 1, p > 0.10; frequency modulation: $\chi^2 = 0.330$. d.f.=1, p > 0.80). There was a non-significant tendency for bowerbirds to mimic calls with a similar amplitude modulation to their own calls ($\chi^2 = 3.18$, d.f. = 1, p >0.05, see fig 3.6).

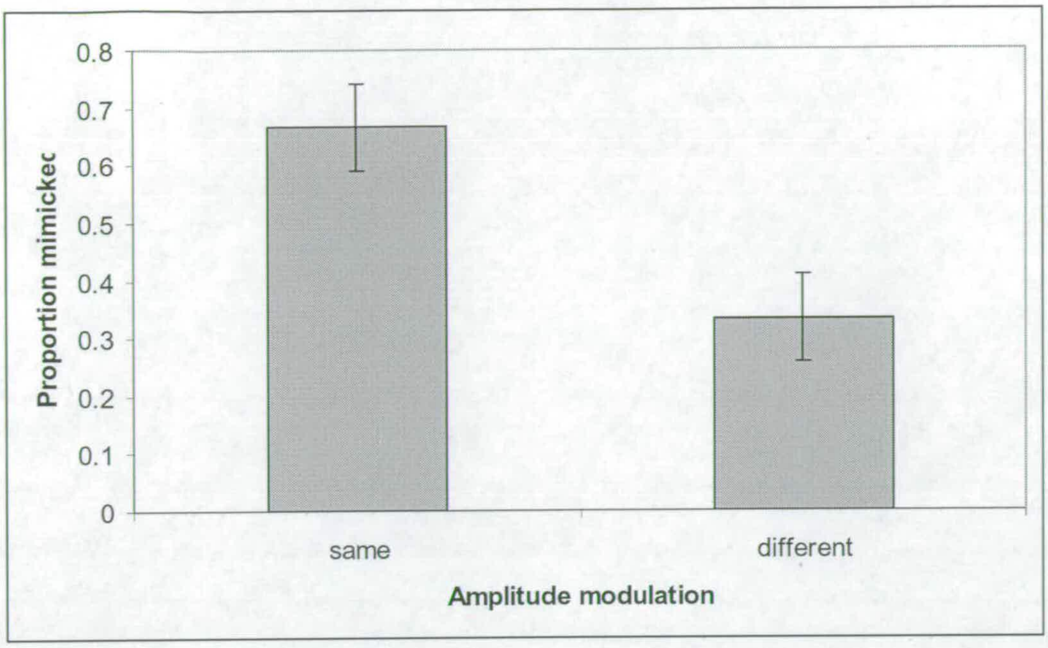


Fig 3.6: Proportion of mimicked calls with the same (n=9) and different amplitude modulation (n=30) as species-specific hiss. (+SD)

The occurrence of mimetic and species-specific vocalisation

Mimicry in the presence of competitors

Mimetic rate tended to be higher in the absence of competitors (GLM: $F_{1,11}$=3.40, p=0.092, see fig 3.7). There was no apparent variation in mimetic rate among bower owners ($F_{25,11}$=0.71,p = 0.766).

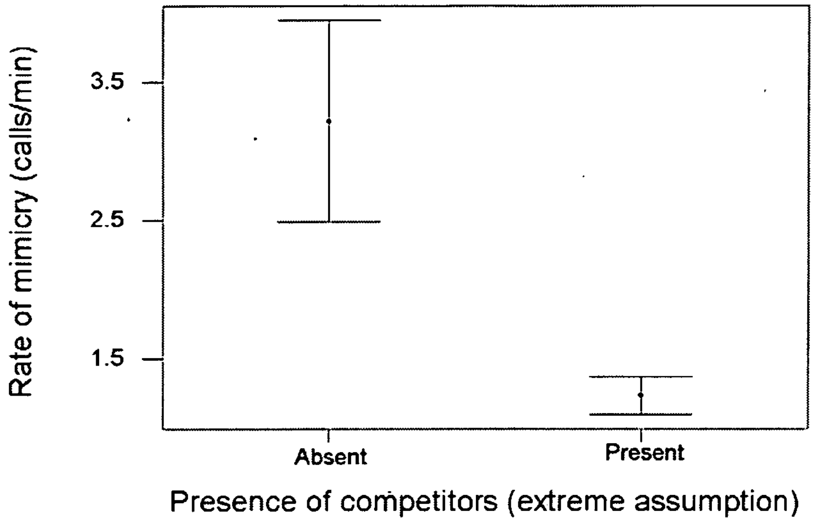


Fig 3.7: Mean rate of mimicry per bird in the presence or absence of competitors (+ SE, n = 12)

Species-specific vocalisation in the presence of competitors

There was no change in the rate of species-specific vocalisation in the presence of competitors (GLM: $F_{1,4}$=0.63, p=0.471,absence: mean +SD=11.02 + 1.38, presence: mean +SD=16.11 + 2.39). There was no difference among individual bowerbirds ($F_{17,4}$=1.01, p=0.560).

Mimicry in the presence of aggressive species

The rate of mimicry tended to increase in the presence of aggressive heterospecifics ($F_{1,16}$=3.44, 0=0.082, see fig 3.8) . No variation among individual bowerbirds was detected ($F_{25,\,16}$= 1.64, p=0.155).

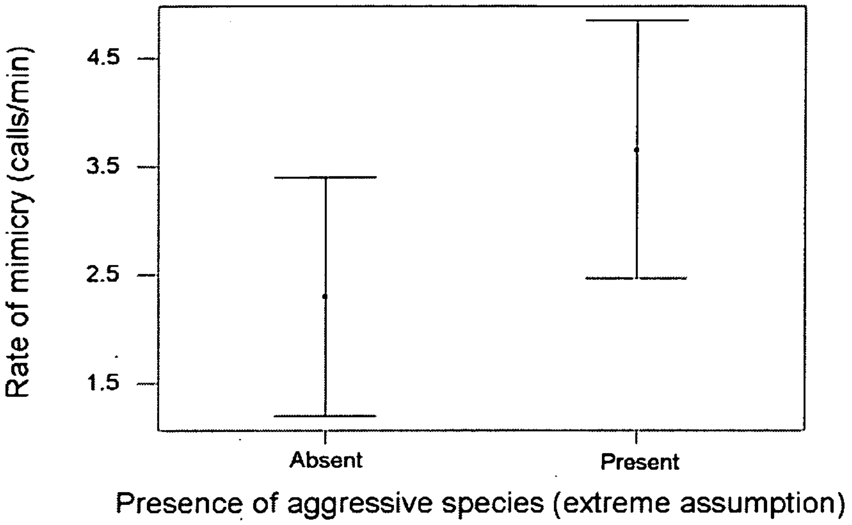


Fig 3.8: Mean rate of mimicry per bird in the presence or absence of aggressive species (± SE, n = 26)

Species-specific vocalisation in the presence of aggressive species

The presence of aggressive species did not alter the rate of species-specific vocalisation ($F_{1,7}$=2.58, p=0.153, presence mean ± SD = 12.975±1.635, absence =12.902 ± 2.108). There was a significant main effect of individual bowerbird ($F_{17,7}$=3.71, p=0.042).

Mimicry in the presence of conspecifics

There was no effect of individual bowerbird (assumption 1), when all vocalisation was considered to belong to the bower owner see 2.13, $F_{28,14}$=0.59, p=0.886) or presence of conspecific ($F_{1,14}$= 0.02, p=0.899) on the rate of mimicry . If however, the mimicry was assumed to be equally shared amongst all birds present there was a marginally non-significant decrease in mimicry in presence of conspecifics (assumption 2), see fig 3.9 $F_{1,14} = 4.30$, p=0.057). Individual bowerbirds still did not differ ($F_{28,14}=0.59$, p=0.886).

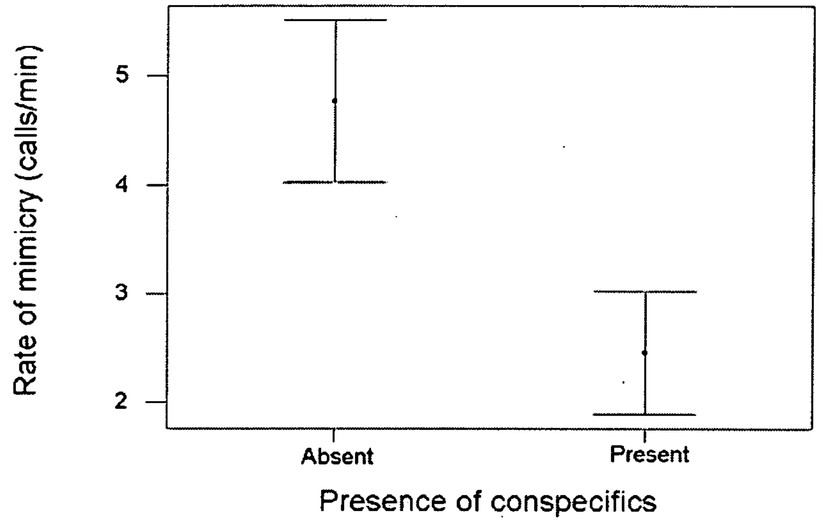


Fig 3.9: Average rate of mimicry per bird in the presence or absence of conspecifics (± SE, using assumption 2 that vocalisation is equally distributed amongst all bowerbirds present, n= 29).

Species-specific hiss in the presence of conspecifics

If all hisses were attributed to just one bird at each bower, then the presence of conspecifics had an effect on the rate of hisses (assumption 1, see fig 3.10, $F_{1,24} = 12.06$, p = 0.02). If, however, the species-specific vocalisation was equally divided between the bowerbirds present there was no effect of presence of conspecifics (assumption 2, $F_{1,24} = 0.19$, p = 0.665). Under neither assumption was there a difference among individuals ($F_{31,24} = 1.44$, p = 0.181).

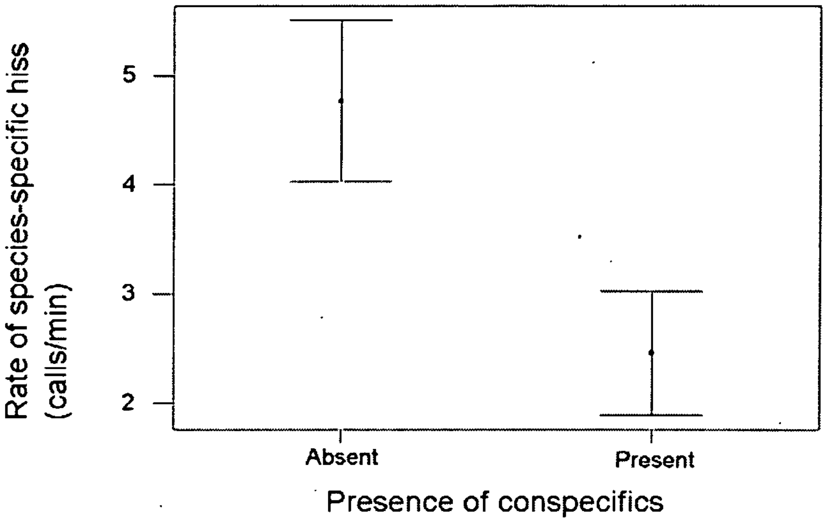


Fig 3.10: Mean rate of species-specific hiss in the presence or absence of conspecifics, using assumption 1 that vocalisation is all attributed to one bird (± SE, n = 32).

Seasonal variation in rate of mimicry

The average rate of mimicry per observation did not alter throughout the field season (see fig 3.11). A GLM using only the ringed bowerbirds recorded mimicking during the observations showed no effect of individual (random factor, 2002: $F_{10,3}$ = 0.45, p=0.85; 2003: $F_{16,11}$ =1.18, p= 0.40) or of the date (co-variate, 2002: $F_{1,3}$= 0.001, p=0.950; 2003: $F_{1,11}$ =2.86, p=0.119). The results were the same for both years combined (individual: $F_{24,18}$=0.86, p=0.636; date: $F_{1,18}$ =1.19, p=0.290). There were too few data to look for interactions. The outcome was the same when the analyses were repeated once five outliers with an average mimetic rate of over 2 calls/min were removed.

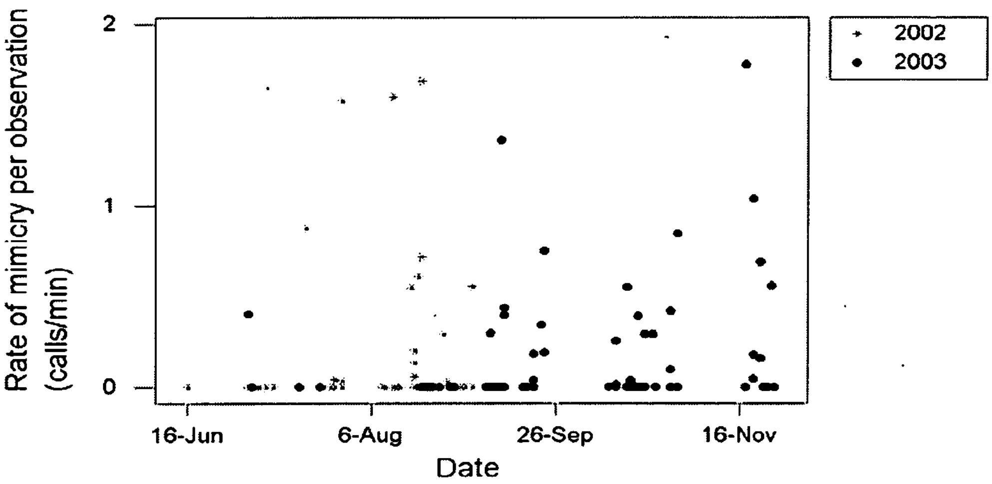
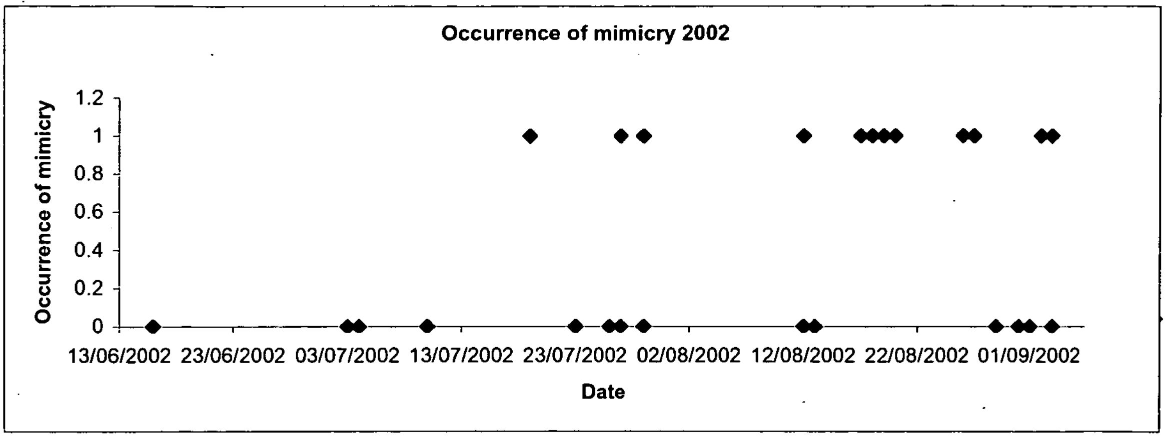


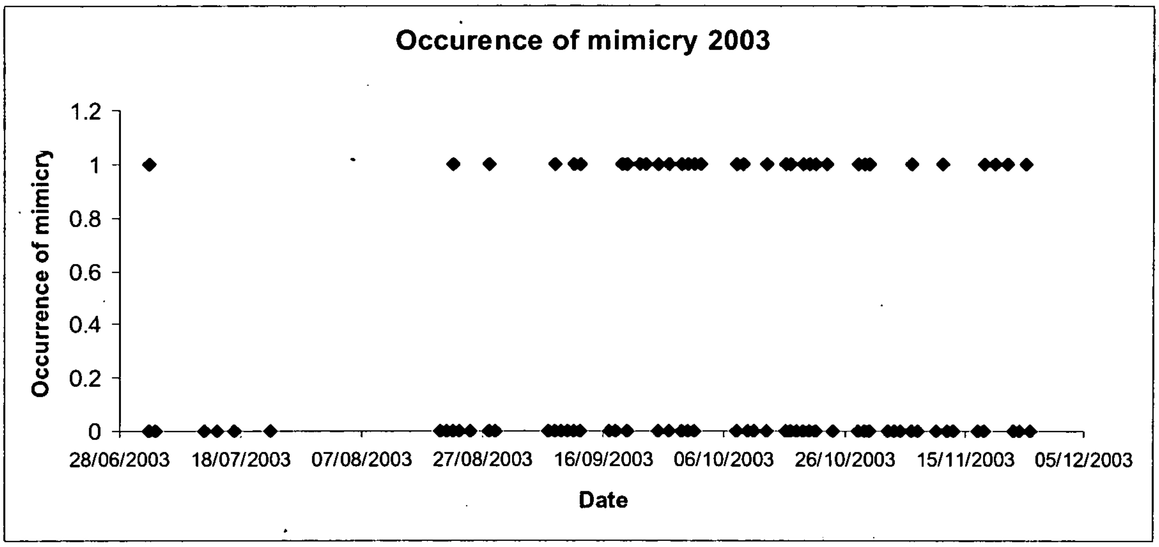
Fig 3.11: Average rate of mimicry per observation over the course of two field seasons (with five outliers removed). NB the lack of points beyond September in 2002 was due to interruption of observational data by experiments.

Seasonal variation in the occurrence of mimicry

In 2002, the occurrence of mimicry during observations showed an increase over the field season. This was not observed in 2003. As a mixed effect model showed no significant effect of individual bowerbird, this factor was dropped from further analyses. A logistic regression showed a marginally non-significant main effect of year ($F_{1,176}$=3.501, p=0.0630) and no effect of date ($F_{1,176}$=0.0385, p=0.845). However, there was a significant interaction between year and date ($F_{1,176}$=6.171, p=0.0139, fig 3.13): in 2002 there was an increase in occurrence of mimicry throughout the season (t=2.526, d.f.=176, p<0.002, fig 3.12 a), whereas in 2003 there was no change(see figs 3.12b).



a)



b)

Fig 3.12: occurrence of mimicry during observations in a) 2002 and b) 2003 field seasons (1 represents occurrence and 0 non-occurrence of mimicry)

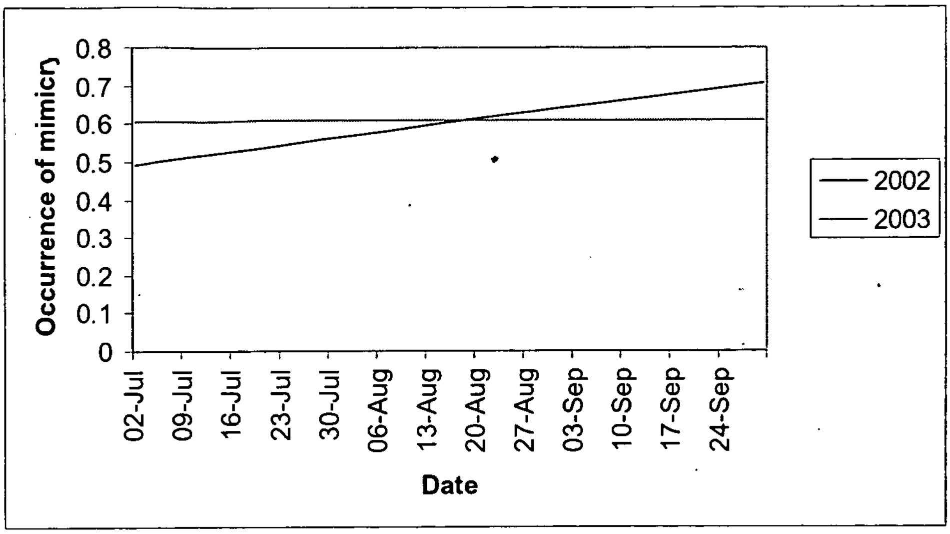


Fig 3.13: Occurrence of mimicry as predicted by logistic regression model (where zero is absence of mimicry during the observation and one is presence of mimicry) showing significant interaction between year and date

There was no obvious relationship between rainfall and rate of mimicry, on either a monthly (see fig 3.14) or daily basis (not shown). Given the rarity of rain it was not feasible to carry out further statistical analysis.

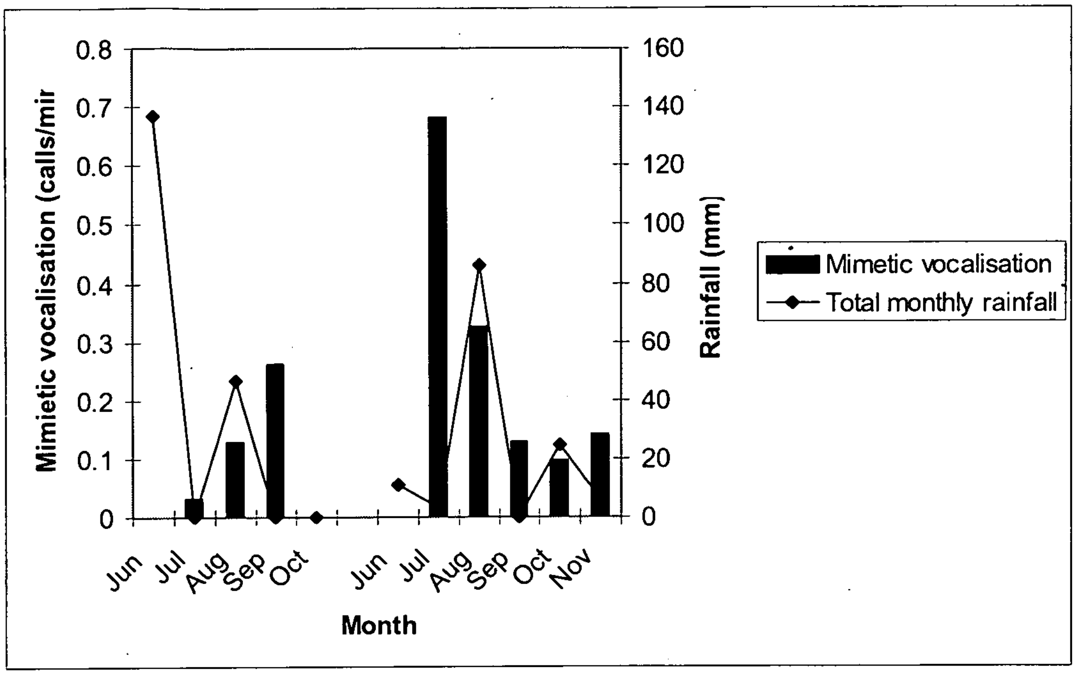


Fig 3.14: Average monthly rate of mimetic vocalisation and total monthly rainfall (2002 and 2003)

Seasonal variation in rate of species-specific vocalisation

In 2003, there was an effect of date on the rate of species-specific vocalisation (GLM, co-variate: $F_{1,20}$=5.00, p=0.037, see fig 3.15), the rate tended to increase over the field season. There was no effect of individual (random effect: $F_{21,20}$=1.43, p=0.216). In 2002, neither date nor individual had an effect on species-specific vocalisation (date: $F_{1,26}$=0.28, p=0.613, individual: $F_{18,26}$=0.70, p=0.745). The analysis was repeated after removing two outliers with an average species-specific rate of over 30 calls/min, which made no qualitative difference to the significance of the results.

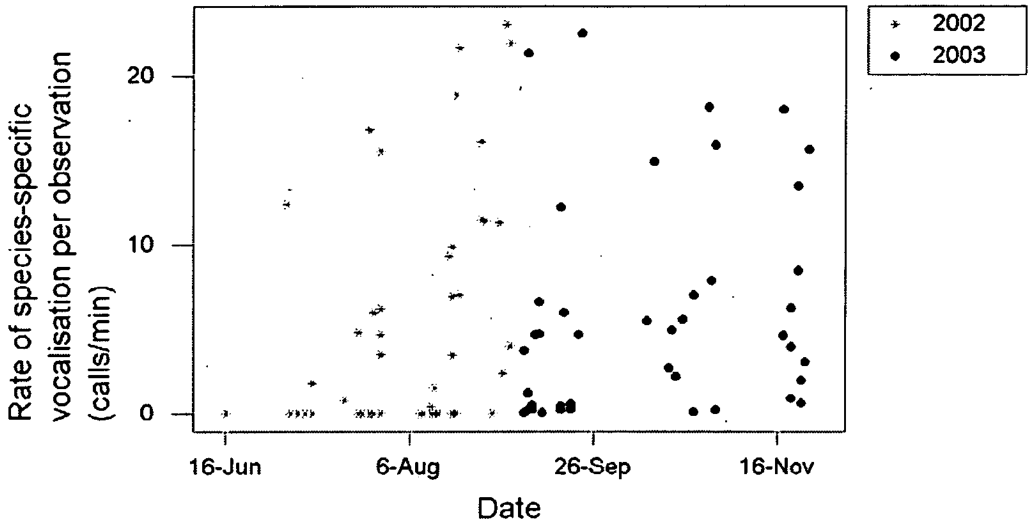


Fig 3.15: average rate of species-specific vocalisation per observation over the course of two field seasons (two outliers removed). (Note: gaps in data due to the later field season in 2003, no record of species-specific rate for July and August 2003 and other interruptions of observations due to experiments.)

As with the mimetic vocalisation, there was no obvious link between rainfall and species-specific vocalisation rate during the observations (see fig 3.16).

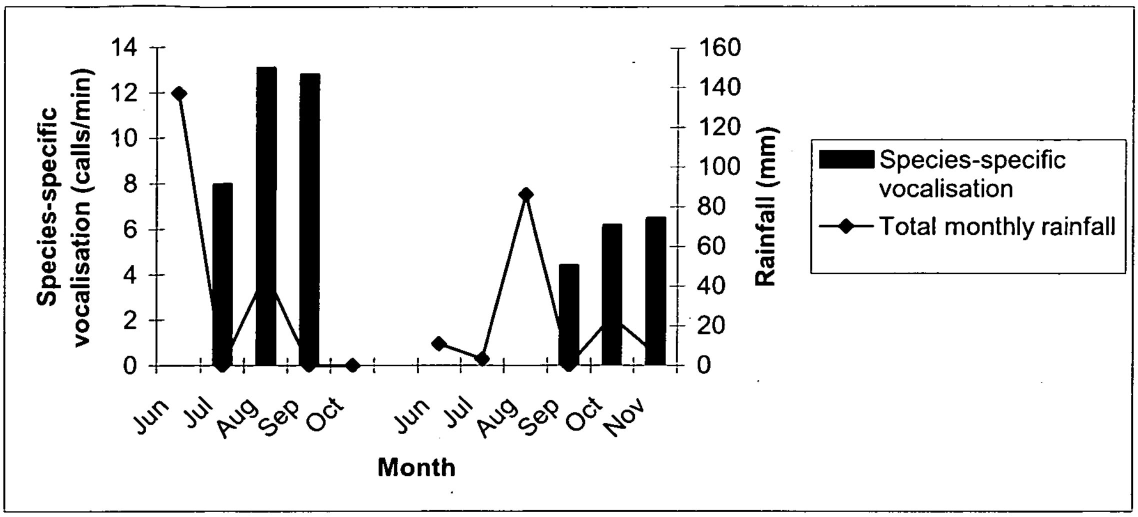


Fig 3.16: Average monthly rate of species-specific vocalisation and total monthly rainfall (2002 and 2003). NB rates of species-specific vocalisation were not calculated in July and August 2003.

Correlation between mimicry and species-specific vocalisation

There was a negative correlation between the rate of species-specific hiss and mimetic calls (Pearson correlation r=-0.425, d.f. = 40, p=0.002, see fig 3.17). The rate of species-specific vocalisation decreased as mimicry increased.

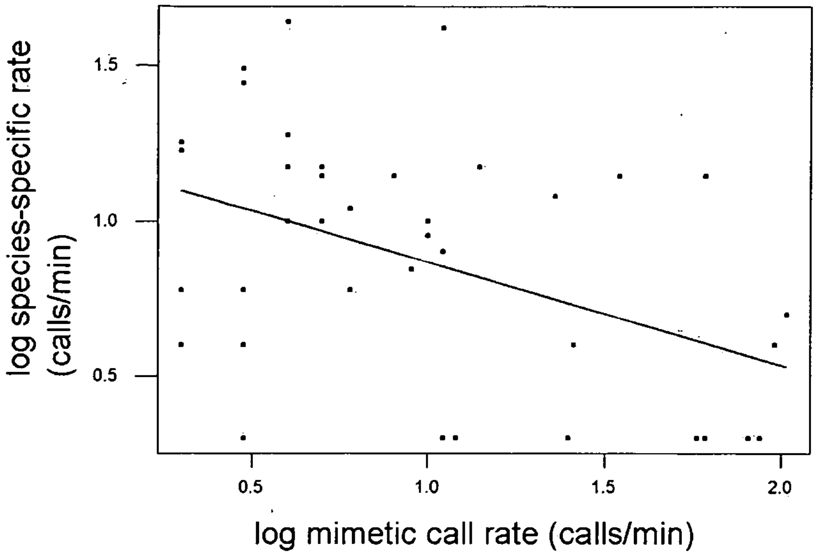


Fig 3.17: Relationship between species-specific and mimetic call rate (log transformed)

3.4 Discussion

Spotted bowerbirds did not mimic commonly heard or simple calls preferentially. There was a slight suggestion that the birds mimic calls that share similar frequency modulation to their own hiss, although they did not preferentially mimic calls that had similar amplitude modulation or frequency structure. Similarity in frequency modulation among species-specific and mimetic calls may arise purely because physiological constraints mean that only a subset of potential models can be mimicked (Kaplan, 1999; Podos, 2001). The negative correlation between rate of species-specific and mimetic vocalisation supported the idea that the function of the two types of vocalisation is different and possibly mutually exclusive. These data, thus, do not fit with the predictions from the Learning Mistakes hypothesis (Hindmarsh, 1986).

As the mimetic rate either remained constant or tended to decrease in the presence of conspecifics, neither the individual recognition (Harcus, 1977) nor the sexual selection hypothesis (Howard, 1974) appear to explain vocal mimicry in these birds. Due to the lack of ringed females (none were observed), it remains a possibility that bower owners could increase their mimetic rate in their presence, however, mimicry has not been noted in courtship displays (J. R. Madden pers comm.). The birds did not preferentially mimic complex calls, which might be expected if females showed a preference for calls that were costly to produce (Gibson & Bradbury, 1985; ten Cate et al., 2002).

None of these observations were consistent with the hypothesis that vocal mimicry is sexually selected in this species. The only evidence to the contrary was a tendency for the occurrence of mimicry to increase over the season and this was only found in 2002. This effect seemed to be due to an absence of mimicry in the earliest observations in 2002, followed by a significant rise in occurrence of mimicry subsequently. The lack of a similar pattern in 2003 may be due in part to the later start of field observations. It is possible that vocal mimicry is involved in initial mating decisions made by the female, whilst other factors, like bower quality, are used to choose her final mate (Coleman et al., 2004). This would explain the very low occurrence of mimicry at the beginning of the 2002 season when bower attendance was also very low. The increased occurrence of mimicry throughout the season could also be consistent with other hypotheses, for instance, if there was an increase in competitors or predators throughout the season. There was no change in rate of mimicry over the field season, nor any obvious relationship with rainfall patterns. Spotted bowerbirds at Taunton usually mate between late October and early November and mating is often preceded by heavy rainfall (Madden, 2001b).

There was no evidence to support the Beau Geste hypothesis (Rechten, 1978): birds did not preferentially mimic food competitors. This was true even when aggressive species were removed from the analyses. The rate of mimicry tended to decrease in the presence of competitors, suggesting that the function of mimicry was neither to deter competitors by making the environment sound more crowded than it was (Beau Geste) nor to scare them off in a form of competitive Batesian mimicry (Dobkin 1979). Although it was not explicitly tested, the mimicry of birds did not appear to attract other heterospecifics (Morton, 1976).

A number of observations were, however, consistent with predictions from the Batesian mimicry hypothesis (Dobkin, 1979). Firstly, contrary to the findings in other species (Howard, 1974; Hindmarsh, 1984; Chu, 2001a, b; Fergusson et al., 2002; Hamao & Eda-Fujiwara, 2004), spotted bowerbirds mimicked more aggressive birds than would be expected by chance. Combined with the observation that the rate of mimicry tended to increase in the presence of aggressive species and to decrease in the presence of competitor species, this result suggests that mimicry might be directed at potential predators and not at competitor species. The increased rate of mimetic vocalisation in the presence of aggressive species was not caused by an increase in overall vocalisation, as was shown by the negative relationship between the two types of vocalisation. However, it should be noted that not all of the spotted bowerbirds' mimicry was that of threatening species. Of the fourteen avian models mimicked, four were of non-aggressive species, so Batesian mimicry alone is not sufficient to explain the occurrence of mimicry in the spotted bowerbird.

The tendency to decrease rate of vocal mimicry in the presence of competitors might be seen because of the increased mimicry in the presence of predators. There was little overlap (two species) between birds in the competitor and aggressive species categories, hence the opposite effect on the rate of mimicry is perhaps to be expected. An increase in mimicry in the presence of non-competitive species usually amounts to the same thing as an increase in mimicry in the presence of aggressive species.

There was some evidence that species-specific vocalisation served a different purpose to that of vocal mimicry. Overall, there was a negative correlation between the rate of species-specific and mimetic vocalisation. The rate of species-specific hiss increased in the presence of conspecifics but only when the number of hisses was divided equally among the individuals present at the bower (assumption 1). Although this could be explained simply by two birds calling twice as often as one, it seemed to me that one bowerbird, usually the bower owner, produced the majority of the vocalisation, hence there really could be an increase in rate of species-specific vocalisation in the presence of conspecifics. There was also an increase in rate of species-specific vocalisation throughout the year, towards the mating season. There was no change in the rate of species-specific vocalisation in the presence of competitive or aggressive species. These observations are all consistent with the hiss being involved in sexual selection in the spotted bowerbird. A previous study showed that males with a greater ratio of long to short hisses during their courtship displays obtain more copulations (Borgia & Presgraves, 1998). There were individual differences in both species-specific and mimetic vocalisation; the significance of this is addressed in detail in chapter 5.

Although there was no support in my data for mimicry of common calls, there are a couple of caveats. Firstly, the birds I defined as commonly heard were perhaps not those most commonly heard by the bowerbird. In particular, my observations were limited to those calls heard during the course of my experiments, i.e. those heard between 6:00am and 5:00pm from June to November. Spotted bowerbirds mimic the bush stone-curlew *(Burhinus grallarius),* which is heard almost exclusively at night (Simpson & Day, 1999) and was never heard during observations. Other models were heard during the observations. Although sensitive periods - during which most song learning occurs (Marler, 1987) - have not been reported for mimetic vocalisation, if there was one this would occur outside of the period studied here (spotted bowerbirds in this population nest around November or December). Hence, juvenile bowerbirds might be exposed to calls at a different frequency to what was recorded here.

Secondly, it is not possible to say which calls are the most salient to the bowerbirds. There is bound to be a bias, when collecting data on occurrence of vocalisations, towards noticing birdcalls which are easily heard and recognised by the human auditory system. Birds commonly heard at other times of the day or year, or that may be especially salient to bowerbird may be under-represented in my sample of environmental noises. Bowerbirds may, therefore copy songs that they hear most often, or most distinctly, even though they do not preferentially mimic the commonly heard calls during observations. I cannot, then, completely exclude the Learning Mistakes hypothesis as an explanation of mimicry in spotted bowerbirds.

The way I measured complexity and similarity among mimicked and non-mimicked calls was obviously limited. The spectrograms I looked at might not be representative of each species, especially in species with varied repertoires, or of the bowerbirds' sound environment. The analysis could be improved by sampling more calls, from different individuals. Various features of these calls could be measured (e.g. maximum frequency, band width and so on) and entered into a Principle Component Analysis (PCA) to see how similar features of the models calls are to the bowerbird species-specific call (Hamao & Eda-Fujiwara, 2004). This approach could also be used to remove species that are beyond the vocal range of the bowerbird from analyses on whether common, predatory or competitor species are preferentially mimicked (Kaplan, 1999). Studies on the actual energetic costs of producing vocal mimicry could also be profitable.

My assessment of seasonal patterns in species-specific and vocal mimicry was also restricted because the collection of observational data was interrupted in both field seasons by experiments. It is possible that these interruptions prevented me from observing existing patterns. From the data collected here, seasonality does not seem to have a strong effect on mimetic vocalisation. To draw any further conclusions, more data would be required on other years and also on the rate of mimicry outside the bower building and maintaining season.

There were insufficient data to assess whether there was a relationship between vocalisation and rainfall. It should be noted that observations had to be suspended on the heaviest days of rainfall and on those directly following due the impassability of the roads, so crucial data that could reveal a pattern were potentially missing. Observational data were also lacking for periods during which experiments were carried out. It is not possible to confidently conclude from my data that rainfall does not influence mimetic vocalisation.

In summary, the most likely explanation for the mimicry of spotted bowerbirds appears to be as a type of Batesian acoustic mimicry. Aggressive model species are preferentially mimicked and the rate of mimicry tends to be higher in the presence of threatening species. Batesian acoustic mimicry has been suggested as a function of avian mimicry previously (Chisholm, 1932; Warham, 1962; Dobkin, 1979; Kaplan, 1999) but as far as I am aware this it the first study that provides more than anecdotal evidence for it. In the next chapter I test the hypothesis experimentally.

Chapter 4. Why do spotted bowerbirds mimic? – Experimental manipulations

4.1 Introduction

Very few experiments have been carried out to determine the function of vocal mimicry. Notable exceptions are studies on phainopeplas (*Phainopepla nitens*) and the mockingbird (*Mimus polyglottus*) that looked for an interspecific function of mimicry. Chu (2001a) presented a predator decoy and played phainopeplas distress calls (which often include mimicry) to determine whether mimicry was used to elicit a mobbing response in the models. Heterospecifics did respond to the playback by mobbing the decoy but were more likely to do so in response to phainopeplas species-specific calls than mimicry. There was no evidence that mimicry was directed at the model species and less than a quarter of the species that mobbed the decoy were mimicked. Playback experiments were also carried out on the potential receivers of mockingbird mimicry. Brenowitz (1982) tested the response of red-winged blackbirds (*Agelaius phoeniceus*) to conspecific calls and mockingbird mimicry of the same calls. They did not appear to be able to distinguish between the calls and responded aggressively to both, demonstrating the accuracy with which mockingbirds can mimic and suggesting that the mimicry could function in interspecific territoriality. However, a further experiment on another potential receiver of mockingbird mimicry, the Florida scrub-jay (*Aphelocoma coerulescens*), failed to replicate these findings (Owen-Ashley et al., 2002). The crucial difference between the two experiments appeared to be in the context of the recordings, the first playing isolated mimicked calls whilst the second played mockingbird mimicry embedded in species-specific vocalisation, as it would occur naturally.

In the previous chapter I found that spotted bowerbirds preferentially mimicked aggressive species and tended to mimic at a higher rate in the presence of these species. This is suggestive that the Batesian acoustic mimicry hypothesis explains the mimicry of the spotted bowerbird, although other hypotheses could not be completely excluded. In this chapter I test whether mounts of stuffed birds, of differing threat value, or disturbances at the bower, elicit mimicry from the bowerbirds. Finally, I attempt to use playback to study potential intraspecific reaction to mimetic vocalisation.

4.2 Presentation Experiment

Birds do not always appear to distinguish between decoys and living animals and many studies have utilized this to test responses to potential mates (Frith & Frith, 1993; Patricelli et al., 2002), competitors (Andersson, 1991; Jablonkski & Matyjasiak, 1997) and predators (Naguib et al, 1999; Alvarez & Sanchez, 2003).

Similarly, K. Munro and J. R. Madden (pers comms.) tested the response of spotted bowerbirds to a mount of a brown falcon (*Falco berigora*) a known predator of bowerbirds (J. R. Madden pers obs.). They found no change in rate of mimetic vocalisation compared to baseline data before the mount was revealed from under a plastic bag. However, the falcon was presented on the ground in front of the bower, which was perhaps not sufficiently realistic for an aerial predator and thus the bowerbirds may not have perceived it as a threat. I, therefore, presented mounts in trees near bowers and compared reactions to three different mounts as well as a control treatment with no mount present. I used mounts of a falcon, a crow and a dove, to assess whether the bowerbirds responded with mimicry depending on the level of perceived threat represented by each model (a known predator, a potential nest predator and a non-threatening, non-competitive heterospecific respectively). I recorded the rates of mimetic vocalisation to test whether there was an increase in the presence of threatening species (falcon and crow) compared to the non-threatening species (dove), as predicted by the Batesian mimicry hypothesis (Dobkin, 1979). I also recorded the species-specific vocalisation, including the advertisement calls (see 2.12; Westcott & Kroon, 2002). These loud hisses are given from a vantage point and might be used to signal to predators that they have been noticed, making them less likely to attack (perception advertisement; Curio, 1978). Alternatively they are used to signal to potential mates and rivals the location of the bower and the attendance of the bower owner (Frith & Frith, 2004).

Methods

Between 9th September and 12th October 2002 I presented 14 bower owners with four experimental treatments (see fig 4.1):

(1) A mount of a Torresian crow (*Corvus orru*), representing an aggressive species, which poses no serious threat to an adult bowerbird but is a potential nest predator. Size: 50cm (average measurement from bill tip to tail tip, Simpson & Day, 1999)

(2) A mount of a brown cuckoo-dove (*Macropygia amboinensis*) representing a non-threatening and non-competitive heterospecific. This mount was a control for the bowerbirds reacting to the unusual stimulus of a stuffed bird in a tree, without particular reference to the type of species. Size: 31.5cm

(3) A mount of a brown falcon (*Falco berigora*), a known predator of adult bowerbirds (J. R. Madden pers obs). Size: 41-51cm

(4) The action of placing a mount in the correct tree was simulated. This provided a control for the disturbance caused by humans moving around near to the bower.

The mounts were attached, using wire, to a naturally occurring tree or shrub at a height of 1-2m (mean=1.43m) and 1-6m (mean=3.22m) from the front of the bower. The mounts were put in place in the absence of the bower owner and the observation period commenced immediately. The mount position was the same for each mount at each bower. The order of presentation was varied among birds (see A.5) and a period of at least 7 days passed between presentations to reduce the possibility of an order effect or habituation.

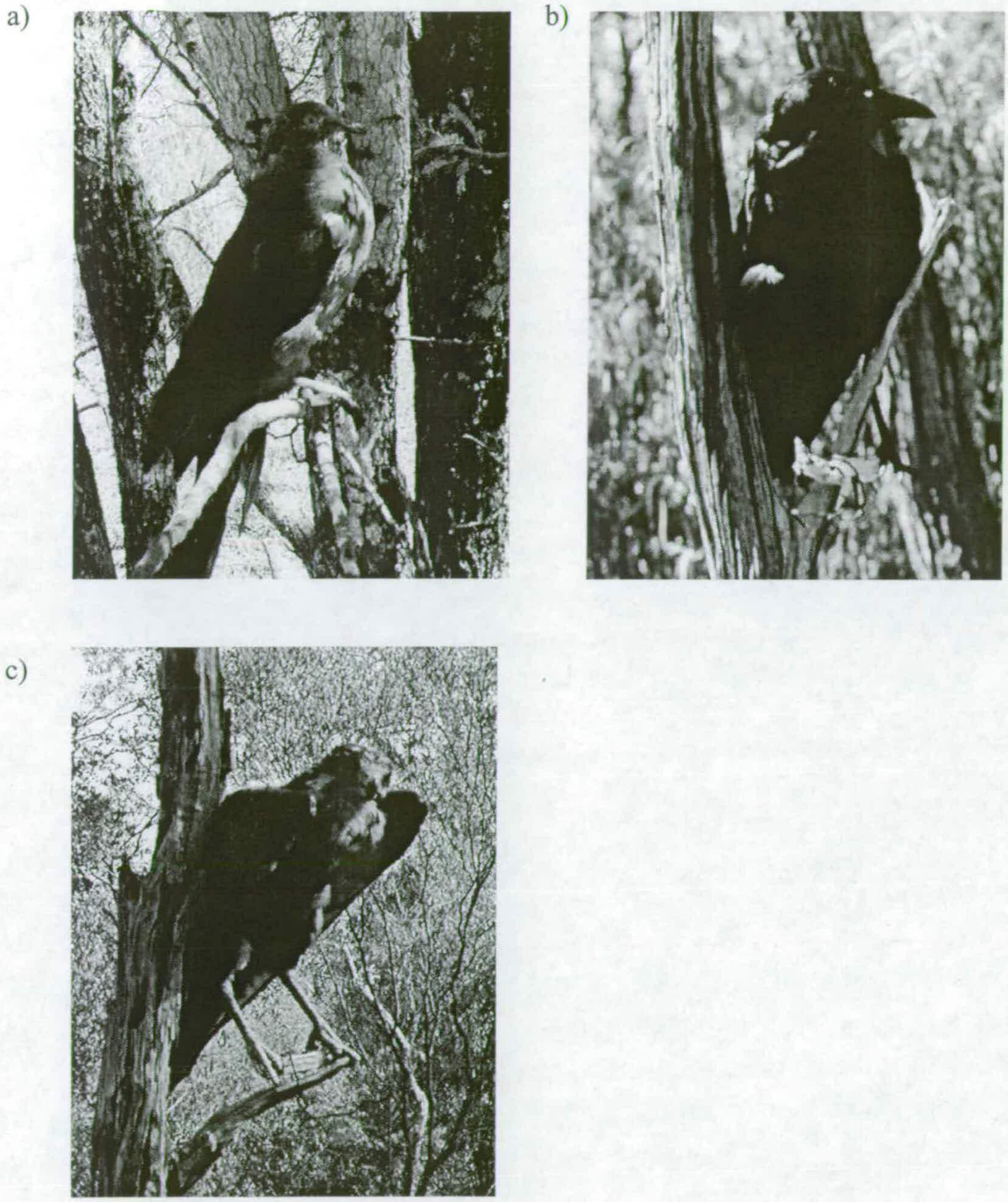


Fig 4.1:Mounts of **a)** brown cuckoo-dove, **b)** Torresian crow and **c)** brown falcon in trees close to the bower

An assistant and I sat approximately 10m from the bower and the mount. We sat separately so that between us we could easily observe the avenue, mount and surrounding area. As before, (see section 2.10) we noted the identity of any bowerbird present, along with its activity, position relative to the bower and mount, and any vocalisations being made. The entire two-hour observation was recorded using a DAT recorder and microphone as described in section 2.11. All observations were made between 6:00am and 11:30am.

From the recordings of the observations, I calculated the rate and type of vocalisations made by the bower owner as described in section 2.13. A mean call rate for each individual under each treatment was then calculated. In addition to the species-specific hiss and mimetic calls, I recorded the number of advertisement calls (a type of species-specific hiss, see 2.12) separately. When more than one bowerbird was vocalising, one of two assumptions were made: 1) either all vocalisations were attributed to the bower owner or 2) calls were shared equally among all bird present (see section 2.13).

The original experimental design was fully cross-factored with each bower owner being shown each mount once. However, due to equipment failure and occasional absence of bower owners, 14 out of the proposed 56 presentations did not occur. One bower owner was not observed at all during the experimental period (see appendix A.5).

Results

Mimetic vocalisation in response to mounts

Use of mimicry was a comparatively rare event; the average rate was 0.44±2.11 (mean ± SD) mimetic calls per minute, with individual averages ranging from 0.023 to 1.29 calls per minute. Mimicry occurred in 19 out of the 42 observations and in nine of the 13 bower owners during this experiment. The rate of mimetic vocalisation among these nine individuals was not affected by the type of mount (GLM: $F_{3,6}$

=0.39, p=0.765, fig 4.2). There was also no individual variation in mimetic rate ($F_{8,6}$=1.11, p=0.461).

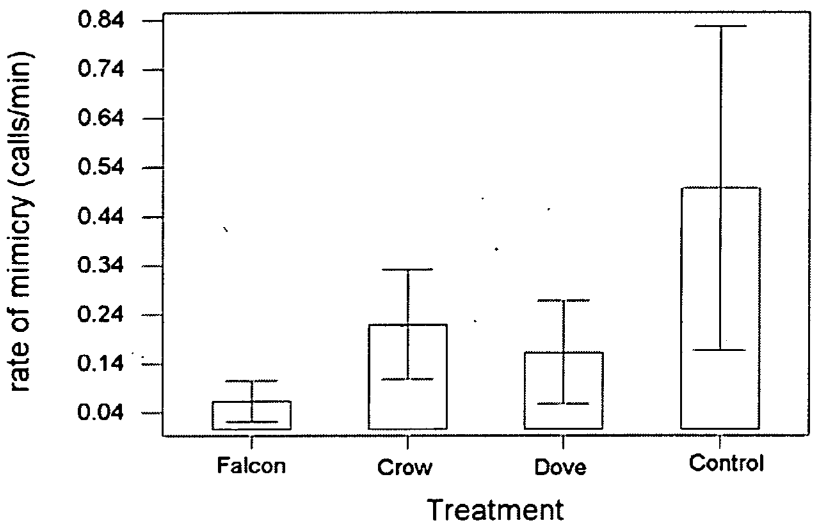


Fig 4.2: Non-significant differences in mimetic call rate (calls/min, mean ± SE) in response to mounts and control treatment.

Species-specific vocalisation in response to mounts

All of the 13 bower owners that were observed during this experiment made species-specific hiss vocalisations. There was a non-significant tendency for species-specific rate to vary in response to the different mounts (GLM: F3,23=2.68, p=0.070, see fig 4.3). There was a significant difference among bower-owners in their call rate ($F_{12,23}$= 3.76, p = 0.003, individual hiss rate varied from 0.64 ± 0.49 to 10.80 ± 6.99 calls/min, mean ±SE).

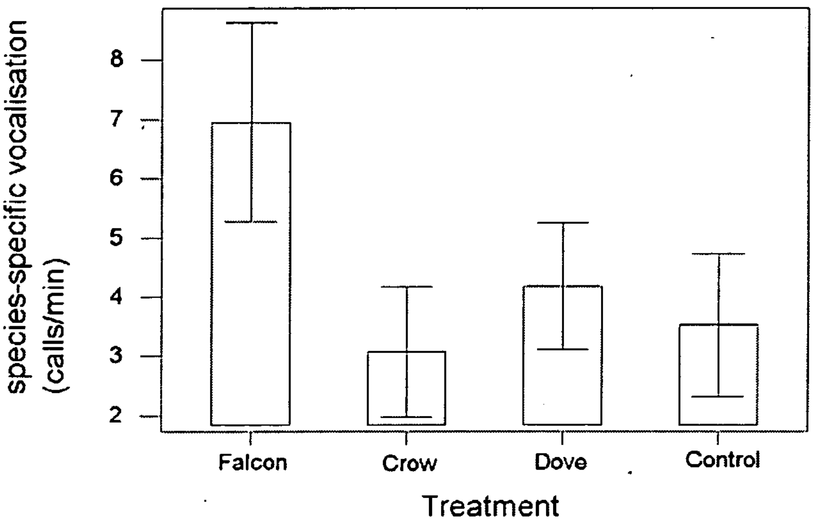


Fig 4.3: Non- significant differences in species-specific call rate (calls/min, mean±SE) for the different mounts and the control treatment

Advertisement calls are a type of species-specific vocalisation but were analysed separately from the species-specific hiss. Only 12 of the bower owners produced advertisement calls during the experiment. There was no evidence that the number of bouts of advertisement calls varied depending on the treatment ($F_{3,18} = 0.25$, p=0.864or the individual bowerbird ($F_{11,18} = 0.99$, p=0.490).

Discussion

Contrary to the predictions of the Batesian acoustic mimicry hypothesis (Dobkin, 1979), bowerbirds did not increase the rate of mimetic vocalisation in the presence of a predatory species. The rate of mimetic calls did not vary in response to any of the treatments. This does not support my previous findings that mimicry tended to increase in the presence of naturally occurring aggressive species and, therefore, could function to scare them off or confuse them (Harcus 1977; Curio, 1978). The lack of change in mimetic rate in response to a model predator is consistent with the previous findings of Munro and Madden (pers comms.).

There was a tendency for different rates of species-specific vocalisation among the treatments. In particular the rate was higher, although not significantly so, in response to the falcon mount, a known predator of adult bowerbirds.Different rates or even types of species-specific calls have been observed in response to predators of differing threats in chickens (*Gallus gallus*, Evans et al., 1993), chickadees (*Poecile* atricapillus, Templeton et al., 2005) and Arabian babblers (*Turdoides squamiceps*, Naguib et al., 1999). These calls could be signals to conspecifics possibly providing information about the type of predator or the degree of threat (Evans et al., 1993; Greene & Meagher, 1998) see also Seyfarth et al., 1980) or pursuit deterrent signals to predators (Curio, 1978; Hasson, 1991; Creswell, 1994).

There were no changes in the number of bouts of advertisement calls in response to the different mounts. If advertisement calls were used as a type of perception advertisement (Curio, 1978) or pursuit deterrent signal (Hasson, 1991), an increase would be expected in response to the mount of a known bowerbird predator, the falcon. An alternative function of these calls is to advertise the location of the bower and the attendance of the bower owner to females and/or rival males, this idea requires testing (Frith & Frith, 2004). Individuals to varied in the rate of species-specific vocalisation. Variation in hiss rate among bower owners is consistent with this vocalisation rate playing a role in sexual selection. Although there was no significant variation in the rate of mimetic vocalisation, four of the thirteen birds tested did not use mimicry at all. Individual variation in vocal characteristics is considered in detail in the next chapter.

This experiment did not test whether mimicry was used to deter competitors either by scaring them off in with a form of Batesian acoustic mimicry (competitive Batesian mimicry: Dobkin, 1979) or by making the environment sound crowded

(Beau Geste: Krebs, 1977; Rechten, 1978). This would require a mount of a bowerbird-competitor, such as an olive-backed oriole *(Oriolus sagittatus)*. Such a mount was not used in this experiment as none were readily available.

Although mounts are often used in experiments (Andersson, 1982; Naguib et al., 1999; Alvarez & Sanchez, 2003), they might not elicit the same response a real predator, competitor or mate. For example, Frith and Frith (1993) noted that the intensity and timing of sexual displays in the toothbill bowerbird (*Scenopoeetes dentirostris*) were different in response to a mount of a conspecific female compared to a living female, although the mount was realistic enough for some males to attempt to copulate with it. In the current experiment, a brown falcon might present a very real threat to a bowerbird but perhaps only in flight, and not when stationary in a tree. However, during the course of this experiment, three other species of birds were observed to mob the mount of the falcon (apostlebird *Struthidea cinerea*, noisy miner *Manorina melanocephala* and pied butcherbird *Cracticus nigrogularis*), so these species at least recognised it as a potential threat. None of the other mounts were ever mobbed. Although mimetic vocalisation did not alter, there was some variation in species-specific vocalisation in response to the different mounts. This suggests the bowerbirds were distinguishing among them and therefore must, at least, be aware of their presence and of their differences. The heightened hissing in response to the falcon might even suggest the bowerbirds did regard these mounts as potential threats.

The use of a single model for each presentation introduces the potential confound of pseudoreplication (Hurlbert, 1984; McGregor, 2000). Thus, the possible increase in species-specific vocalisation I saw in response to the brown falcon might have been specific to that mount and not representative of responses to brown falcons, or other raptors. The use of several different mounts of the same species would improve any repeats of this experiment. Furthermore, combining playback of calls with the presentation of a mount or having a moving model might enhance the realism of the threat.

Another potential problem was the presence of human observers throughout the experiments. We might have disturbed the bowerbirds so that their vocalisation rates differed from the baseline rate under truly natural conditions (Frith & Frith, 2004). However, Madden (2001b) found no effect on the proportion of bowerbird behaviours displayed when observations were recorded either by motion-activated video cameras or by human observers. Also, any effect of human observers should have affected all the treatments equally.

It would be very interesting to carry out a similar experiment to this on nesting females, as there are anecdotal reports of them mimicking when disturbed at the nest (Chisholm, 1937; Warham, 1962). Their vocal reaction to nest predators (species-specific or mimetic) would be expected to be greater than that observed in male bower owners.

There was no support from this experiment that the mimicry in the spotted bowerbird is a type of Batesian mimicry. Presentation of a known predator failed to elicit a higher rate of mimetic calls. However, species-specific hiss calls tended to increase in response to the mount of the falcon, suggesting these might be used in interactions with predators, as a signal to conspecifics or the predator itself.

4.3 Disturbance experiment

Mimetic vocalisations might be given in response to disturbances, including those caused by humans (Dobkin 1979). There is anecdotal evidence that spotted bowerbirds mimic in response to human disturbances (Marshall, 1954; Frith & McGuire, 1996) but this has not been examined experimentally. Chu (2001b) quantified mimicry in phainopeplas (*Phainopepla nitens*) during capture in mist nets and subsequent handling. Although there was no tendency to preferentially mimic aggressive species, Chu suggested the mimicry might have a function in distracting or startling potential predators. Several studies simulate predator attacks by using humans to cause a disturbance (e.g. in screech owls, *Otus asio,* Sproat & Ritchison, 1994; red squirrels, *Tamiasciurus hudsonicus*, Greene and Meagher, 1998 and rufous bush chats, *Cercotrichas galactotes,* Alvarez & Sanchez, 2003). Woodland et al. (1980) observed the response of Eastern swamphens (*Porphyrio porphyrio*) to humans walking at a slow pace towards them. They assumed that the birds' responses (craning, tail-flicking and retreat) to a human were typical of responses to ground dwelling predators and that these behaviours were actually pursuit-deterrent signals directed at the "predator".

I tested the response of spotted bowerbirds to a human disturbance at the bower and compared the rate of mimetic and species-specific vocalisation before, during and after the disturbance.

Methods

Between the 25th September and 10th October 2003, 27 experimental trials were carried out at 19 bowers. I sat approximately 10m from the front of the bower with a clear view of the avenue, whilst a research assistant sat 20m from the opposite side of the bower. When a solitary bowerbird had appeared within 5m of the bower, been accurately identified and remained there for two minutes, a signal, unlikely to have been heard by the bird, was relayed to the research assistant using VHF radios. My assistant then approached the bower, as directly as possible, at an approximate walking speed of 1m/sec. They remained approximately a metre from the bower for 20 seconds before turning round and walking back to their original position. The whole disturbance lasted about one minute. A further two minutes' observation followed the disturbance.

I attempted to increase the number of within-bird replicates by carrying out multiple disturbances on the same bird for the duration of the time it was present.

Although this then meant that the birds' subsequent responses were likely to be affected by recent prior experience, it was logistically difficult to carry out within-bird replicates on different days, due to the distance between different bower sites and the attendance of bowerbirds at bowers at this time being very low (mean time spent within 10m of bower ± SE = 11± 2.53min/hour of observation). The data from the first disturbance were analysed separately in order to remove any effect of multiple disturbances.

Each session lasted 90 minutes, during which between one and 16 disturbances were simulated. 17 individual bowerbirds were tested at 16 bowers, 15 of which were bower owners and two of which were ringed auxiliaries. In cases where no disturbance was made, due to birds not being present long enough to meet the criteria of the experiment, the bower was returned to on a subsequent day. There were three bowers where the criteria were never met and these are not considered in subsequent analyses.

All vocalisations were recorded and I noted the behaviour of the bowerbird before, during and after the simulated disturbance including any mimicry and species-specific hisses and the position of the bird relative to the bower (2.10). Field notes and recordings were used to later identify and count occurrences of mimicry and species-specific vocalisation, recording these as a rate per minute (2.13). Spectrograms produced on Avisoft SAS LabLight were used to assist with the identification of mimetic calls (see 2.13). If a bird flew off to more than 20m from the bower during the disturbance or in the following two minutes these time intervals were removed from the analyses, as it was possible the birds were vocalising but were too far away to be recorded.

Results

Response to the first disturbance

Only four of the 17 birds tested mimicked in response to the first disturbance (see fig 4.4). There was no effect of time interval (i.e. minute 1, 2, 3, 4 or 5; GLM: $F_{4,12}$=1.43, p=0.283) or individual ($F_{3,12}$=1.47, p=0.272) on the rate of mimicry. Of the four birds that mimicked during some part of the disturbance three did so when predicted i.e. minute 3,when there was a human at the bower.

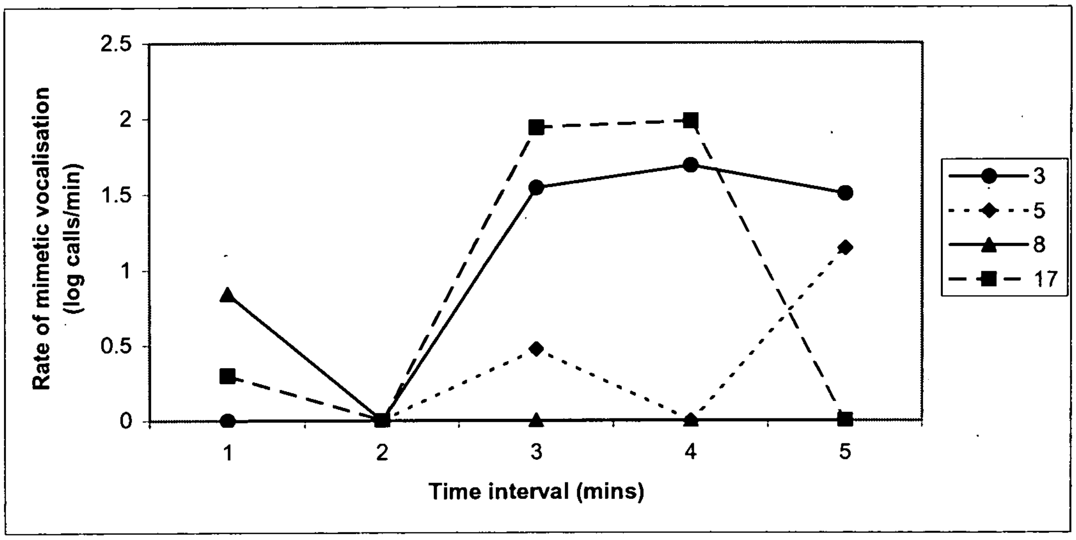


Fig 4.4: Mimetic vocalisation rate during the before (minute 1 and 2), during (3), and after (4 and 5) the first disturbance event, (n=4, the other 13 birds did not mimic at all, for numbering of individual bowerbirds see 5.1 and appendix A.7) Data are shown on a log scale due to very high rates of mimetic calls (e.g. 96 mimetic calls per minute from individual 17 during minute 4).

All 17 birds tested made some species-specific hisses during the course of the first disturbance event and there was individual variation in the rate ($F_{16,54}$=1.90. p=0.041). The time interval was marginally non-significant ($F_{4,54}$=2.41, p=0.060, fig 4.5) with a tendency for vocalisation to decrease after the disturbance event.

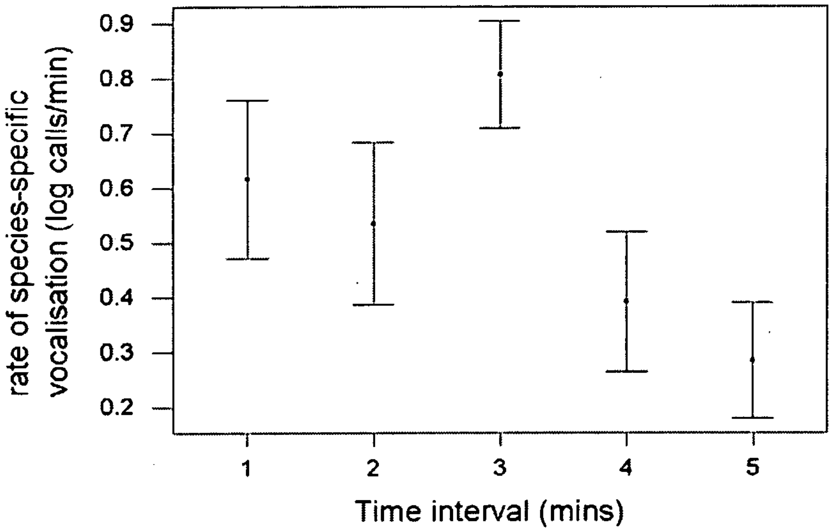


Fig 4.5: Species-specific vocalisation before (1,2), during (3) and after (4 and 5) the disturbance event (mean ± SE, n=17)

Responses to all disturbances

When the data from all of the 60 disturbances were included, mimicry occurred on 23 occasions. However, these responses came from only seven of the seventeen birds tested. The mean rate of mimicry for each one-minute time interval was calculated for each individual of this subset of birds and this was used as the response variable (log transformed) for GLM analysis. The mean rate of mimetic calls varied over the course of the simulated disturbance, peaking during the disturbance and decreasing after it (GLM: $F_{4,24}$=2.90, p=0.043, fig 4.6). There was also significant variation among individuals ($F_{6,24}$=4.31, p=0.004). There were insufficient data to test for an interaction, but the five males that mimicked during the disturbance event showed a tendency to increase mimetic vocalisation rate in minute 3 followed by a steady decline during minutes 4 and 5 (see fig 4.7). There was no significant interaction between time interval and individual if minutes 1 and 2 were pooled as "before" and

3 and 4 as "after" ($F_{6,8} = 1.41$, $p = 0.317$) suggesting that individuals do not react differently over the course of the disturbance event.

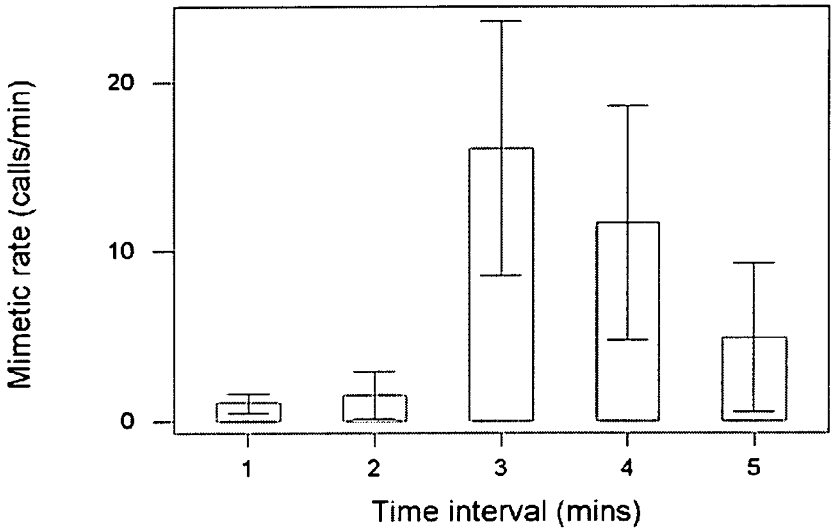


Fig 4.6: Rate of mimicry before (1,2), during (3) and after (4 and 5) the disturbance event (mean ± SE, n=7)

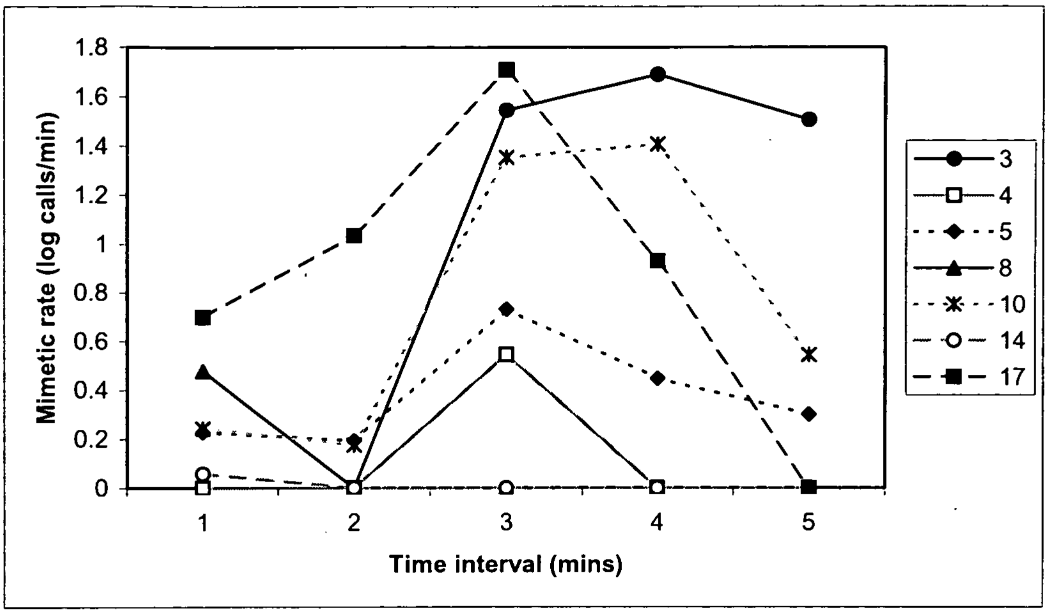


Fig 4.7: Mean mimetic vocalisation rate during the period before (minute 1 and 2), during (3), and after (4 and 5) the disturbance event, (n = 7, for numbering of individual bowerbirds see 5.1 and appendix A.7)

Paired t-tests were carried out to compare the mean mimetic rates per minute before (i.e minutes 1 and 2), during (3) and after (4 and 5) the disturbance for the seven birds. Mimetic rate was higher during the disturbance than before (t=-2.61, d.f. =6, p=0.04). There was no difference between mean mimetic rate before and after the disturbance (t=-1.01, d.f. =6, p=0.351). The mean mimetic rate during compared to after the disturbance was verging on significant, indicating a tendency for mimicry to be lower after the disturbance (t=-2.05, d.f. =6, p=0.087).

There was no significant variation in average species-specific vocalisation over the course of the simulated disturbance events (time interval: $F_{4,55}$=1.49, p=0.218). However, there was variation in hiss rate among the 17 individuals ($F_{16,55}$=2.86, p=0.002). As found in 3.3, there was a negative correlation between mimetic and species-specific vocalisation rates (Pearson correlation: r= -0.449, d.f. =54, p=0.001).

Vocalisation and flight responses

Birds that mimicked were less likely to fly off during or after the disturbance than individuals that gave only species-specific vocalisation or remained silent during the disturbance (fig 4.8, $\chi^2=11.565$, d.f. =2, p=0.003).

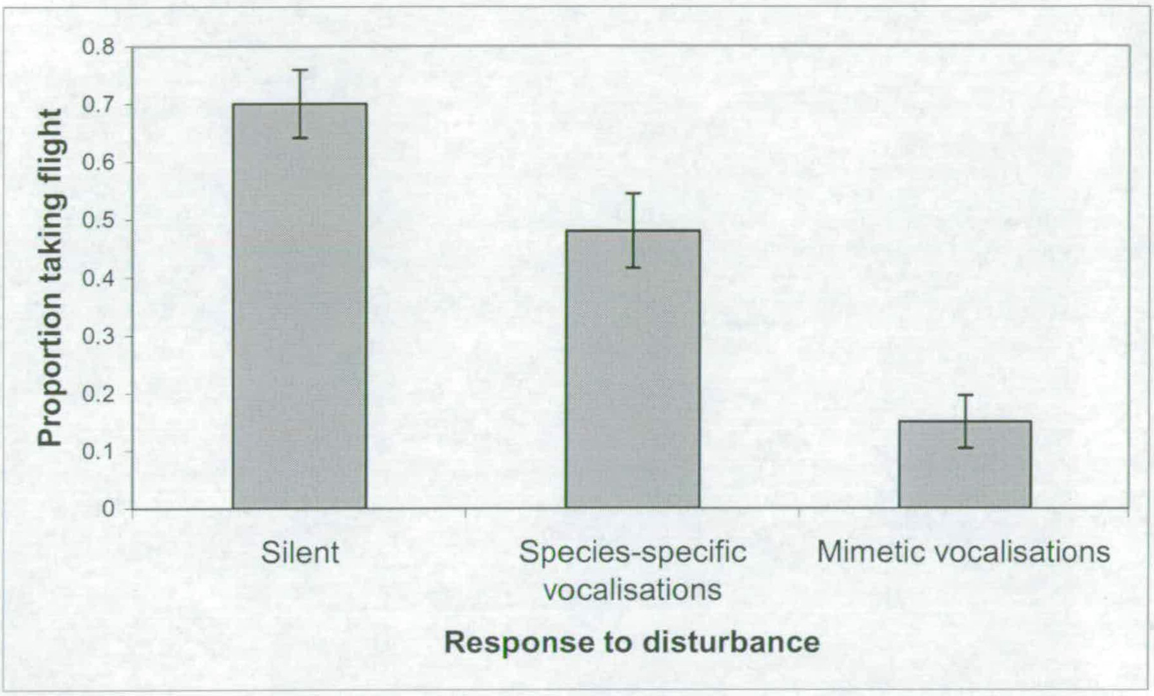


Fig 4.8: Proportion of disturbances (± SE) during which the bird takes flight in each of the different vocal response categories (silent: n= 13; species-specific: n=24; or mimetic vocalisation: n=23)

Individual differences in reaction to disturbance

There was significant individual variation in both average rate of mimicry and species-specific vocalisations (GLM: mimetic, $F_{6,24}=4.31$, p=0.004, species-specific, $F_{16,55}=2.86$, p=0.002). There was also variation in the use of mimicry between individuals; only seven out of the seventeen birds observed mimicked at all during the course of the experiment and just five of these mimicked during the disturbance.

There appears to be a tendency for certain birds to react to the disturbance with a particular strategy, some usually mimicking while others usually producing only species-specific vocalisation (fig 4.9). However, due to a limited sample size and unbalanced data (only 8 individuals were tested more than 3 times and of these there is a large amount of variation (from 3 to 16) in the number of disturbance events) statistical analyses are not viable.

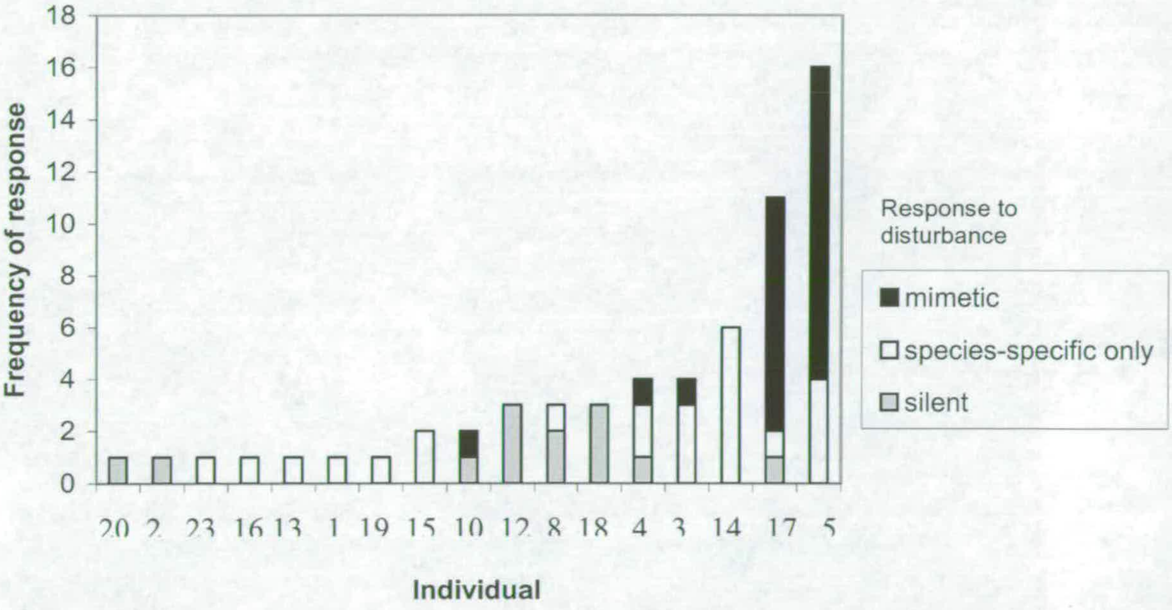


Fig 4.9: Frequency of the different vocal responses (mimetic, species-specific or silence) to disturbances (i.e. during minute 3).

Variation in rate of vocalisation with number of disturbance events

There was no significant correlation between mimetic call rate and the number of disturbance events (Pearson correlation: r=-0.093, d.f. =133, p=0.281). Species-specific vocalisation tended to increase with the number of disturbances but this was marginally non-significant (Pearson correlation: r=0.116, d.f. =270, p=0.055)

Discussion

Five out of 17 bowerbirds used mimicry in response to a human walking towards them at the bower. In these instances there was an increase in mimetic vocalisation rate during the disturbance, which tended to decrease over the following two minutes towards the level observed prior to the disturbance. There was similar, although non-significant, trend when only the first disturbance was considered. This increase in mimetic vocalisation in response to a disturbance is consistent with the idea that mimicry might be used in threat avoidance as a type of Batesian acoustic mimicry (Dobkin, 1979). However, there were considerable differences among individuals with the majority of birds not using mimicry in response to the disturbance.

Species-specific vocalisation did not differ in rate across the disturbance event, except during the first disturbance where there was a non-significant tendency to increase with the disturbance and then decrease afterwards, to levels below those observed before the disturbance. Species-specific vocalisation was negatively correlated with mimetic vocalisation, suggesting that the observed increase in mimicry during the disturbance was not caused by an overall increase in vocalisation. This supports observations in the previous chapter that the two types of vocalisation might perform different functions.

There appeared to be alternate strategies in response to threat such that birds either mimic while remaining near the bower or they flee in silence. Individuals that only produce species-specific hisses are equally likely to fly off or to stay. The use of mimicry when remaining near the bower is consistent with the hypothesis that mimicry is being used as a type of Batesian mimicry and the intended receiver is the predator (Dobkin, 1979). However, this result might be biased by the inclusion of 29 disturbances of two bower owners (individuals 17 and 5 in fig 4.9) that seemed especially prone to remaining near the bower and using mimicry in response to the disturbance. Although the evidence is limited, it is possible that individual spotted bowerbirds tend to adopt the same threat avoidance strategy in repeated disturbances. When skylarks (*Alauda arvensis*) are faced with attack from a merlin (*Falco columbaris*), the optimal strategy for the best quality individuals is to sing and demonstrate their vigour whereas poorer quality individuals are better off remaining silent and seeking refuge (Cresswell, 1994). Something similar might happen in bowerbirds, perhaps only the best quality males are able to produce accurate mimicry that deceives predators. Alternatively, different reactions to human disturbance among individuals could be explained by differing experience with humans and hence differing perception of the degree of threat they pose. This is clearly speculation and these ideas would need rigorous testing once the function of mimicry in the spotted bowerbird is better understood.

It should be noted that the sample of birds that responded to the disturbance with mimicry is small (five out of 17, 29%). There are three possible interpretations of this: (1) the use of mimicry is either confined to only a few individuals in the population (however, this is not consistent with my observational data on 20 bower owners that all mimic, chapter 5); (2) different males use mimicry in differing contexts; (3) not all males perceived the human standing at their bower as the same degree of threat. The latter seems possible as 12 males flew away in response to at least one of the human disturbances suggesting that the disturbance was considered by some males so great that they were not prepared to use mimicry as an attempted deterrent, if this is its function. Chu (2002a) also found variation in the occurrence of mimicry in phainopeplas, although the proportion mimicking during capture and handling was higher than among the bowerbirds (138 out of 206, 67%). I also observed individual variation in the rate of species specific and mimetic vocalisation, as well as occurrence of mimicry (see chapter 5)

Humans might not represent any kind of threat to spotted bowerbirds. Unlike the swamphens in Woodland et al.'s (1980) experiment, which are described as being very wary of people, spotted bowerbirds are not timid and often have close interactions with humans, for example entering houses to steal decorations for their bowers (Frith & Frith, 2004). Observations of behaviour at bowers recorded by a human observer or a hidden camera did not show significant differences (Madden, 2001b), suggesting that bowerbirds are not overly disturbed by the presence of humans. However, a human sitting quietly at the bower is not the same as one walking towards the bird at the bower and the birds evidently reacted to this procedure. What is not clear is whether their reactions are typical of those evoked by real predators, although the increased rate of mimicry in the presence of naturally occurring aggressive species suggest they might be (3.3).

Spotted bowerbirds are probably under the greatest threat from avian predators but feral cats are quite prevalent within Taunton and have been known to take adult birds (J. R. Madden pers obs), so terrestrial threats are not unrealistic. In the evolutionary past, bowerbirds would have probably also been predated by now-extinct marsupial carnivores (Humphries & Ruxton, 1999). Each of the bowerbirds used during this disturbance has had at least one experience with humans that might have been aversive. They have all been caught in mist nets, measured and ringed and some have also had blood and feather samples taken (Madden, 2001b).

The greatest limitation in using humans to simulate predators is that the experiment provides no information on how a predator reacts to the mimicry of the bowerbird (Hasson, 1991). To conclusively demonstrate that spotted bowerbird mimicry is a type of Batesian mimicry the reaction of real predators need to be studied. In particular, evidence of potential predators being deterred or impeded during attack by mimetic vocalisation is required.

I tested individual birds more than once to see whether there were consistent individual differences. Ideally, tests would have been carried out several days apart to avoid habituation but this was not logistically possible. However, there was no evidence that habituation occurred, as there were no changes in vocalisation rates over multiple disturbances. A larger sample size and more repeats on individuals would be necessary to see how widespread the use of mimicry is and would also give information on whether alternative strategies in response to threats really exist.

In contrast to the presentation experiment (4.2), the disturbance experiment does provide some support for the Batesian mimicry hypothesis. Some individuals respond to threats with mimetic vocalisation and the "predator" might even be the intended receiver. However, there are considerable individual differences in the use of mimetic vocalisation, with the majority of birds not being observed to mimic in response to a disturbance. Other individual differences in vocal traits are considered in the next chapter.

4.4 Playback experiment – pilot study

The disturbance experiment (4.3) suggested a potential interspecific function of vocal mimicry: that of Batesian mimicry in response to threats. However, this does not exclude the possibility that mimicry serves intraspecific functions too. Many experiments involve playing calls through speakers to gauge individuals' responses. For example to determine whether territorial birds recognise the calls and appropriate location of their neighbours (Weden & Falls, 1959), to test female preference for repertoire size (Gentner & Hulse, 2000) to assess the occurrence of individuals for conservation purposes (Kennedy & Stahlecker, 1993) or to test heterospecifics' reactions to mimicry (Owen-Ashley et al., 2002).

If mimicry has a function in mate choice and/or male-male competition, conspecifics need to be able to distinguish between mimetic and model calls. Females might then be attracted, and rivals deterred, by males with large mimetic repertoires. I intended to test this idea using playbacks of bowerbird mimicry.

However, I had to first determine whether bowerbirds would respond to recordings of calls in a manner I could detect and measure. The following pilot study was used to look at birds' reactions to a playbacks of models and mimicry. A variety of different calls were used to maximise the chances of recognising any response.

Methods

Between 2nd and 17th November 2003 a pilot study for potential experiments using call playbacks was carried out. I sat approximately 10m from the bower with a clear view of the avenue; an assistant sat 10m the other side of the bower. As with the disturbance experiment (4.3), when a bowerbird had arrived within 5m of the bower, been identified and remained present for two minutes, I sent a signal to my assistant using VHF radio. This was the cue to begin the playback. The playback consisted of one of three different types of sounds all recorded using a DAT recorder and played back using a Sony Walkman minidisk player (see 2.11) and speakers. To reduce possible effects of pseudoreplication there were three examples of each sound type, taken, where appropriate, from a different known bowerbird or three different recordings of white noise. The sounds played were as follows:

1. Species-specific – three examples of simple hissing and three of display hissing (see 2.12)
2. Mimicry – three examples of each of butcherbird, babbler and brown falcon mimicry
3. Control – three examples of white noise, a biologically insignificant noise to control for the novel stimulus of sound coming from speakers

Each playback consisted of just one call type lasting one minute, when a call did not last this long it was repeated accordingly. After the recording was played, a further two minutes' observation was carried out. There was a 72 hour period before another playback was carried out at the same bower.

The type and example of sound was changed see A.6) among bower owners and to minimise the risk of habituation a period of at least 72 hours elapsed between playbacks at each bower. 19 bowers were used for this experiment. There were 28 attempted trials, only 13 of which resulted in bowerbirds being present within 5m of the bower for long enough for the playback to take place. As there was an apparent lack of response to the playbacks (see table 4.1), the proposed repeats of the experiment were not carried out as planned.

As described previously the behaviour and vocalisation of birds was noted and sound recordings were made using a DAT recorder (see 2.11). In addition to the usual behavioural observations the bird's position relative to the speakers was noted, for each minute of observation the bird could either approach or retreat from the speakers or remain in the same place. The number and type of vocalisations made by the bowerbird were subsequently identified from the sound recordings, using Avisoft SAS Light to create spectrograms to assist with this process.

Results

Mimetic vocalisation in response to playback

Mimicry only occurred in five one-minute intervals in the entire experiment, these cases are recorded below but there were insufficient data for further statistical analysis.

			Event relative	Mimetic vocalisations (call rate/min)					Position relative
Date	Bower	Playback	to playback	babbler	magpie	noisy miner	cat	total	to speakers
06/11/2003	19	hiss 1	after	7	0	0	0	7	remained the same
12/11/2003	17	butcherbird 3	after	0	1	0	0	1	remained the same
13/11/2003	21	control 1	before	0	0	8	0	8	remained the same
13/11/2003	21	control 1	during	0	0	3	0	3	remained the same
13/11/2003	21	control 1	after	0	0	0	1	1	remained the same

Table 4.1: Incidences of mimicry during Playback Experiment

Species-specific vocalisation in response to playback

Six of the 13 birds tested during this experiment did not make any species-specific vocalisations before, after or during the playback. These were removed from the following analysis. A General Linear Model was used to test whether the rate of species-specific calling varied over time during the experiment (i.e. 5 one-minute intervals) and whether there was any individual variation.

Species-specific vocalisation did not change in response to the playback of calls ($F_{4,11}=0.74$, $p=0.583$, see fig 4.10). There was, however, significant individual variation in species-specific call rate ($F_{6,11}=18.30$, $p<0.001$).

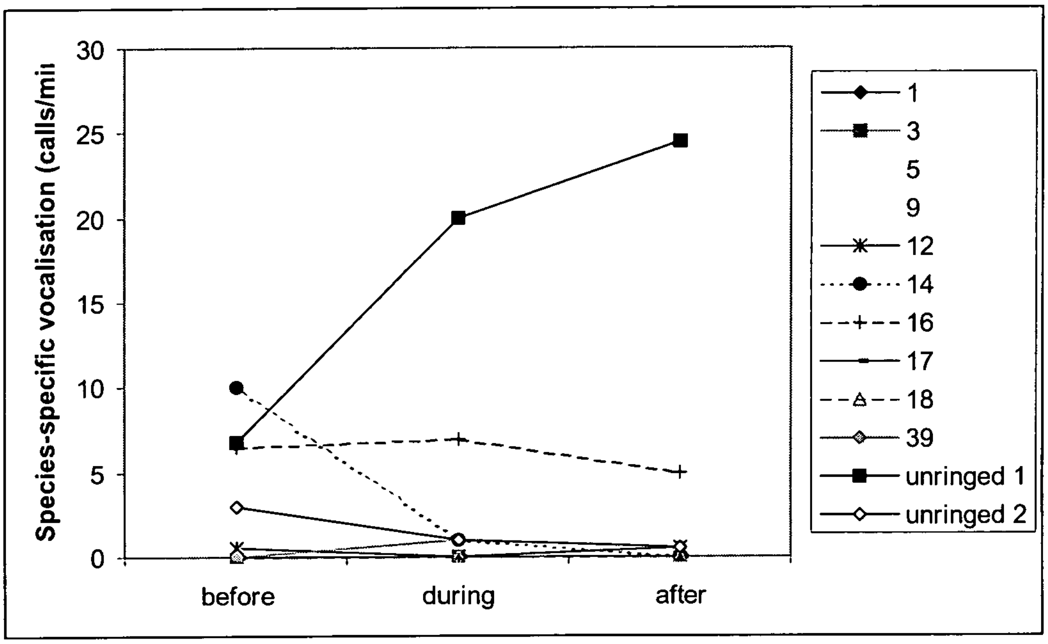


Fig 4.10: Plot showing species-specific vocalisation before, during and after playback (see Appendix A.7 for numbering of individuals).

Approach or retreat from the sound source during playback

For each minute of observation the birds were categorised as approaching towards or retreating from the sound source, or remaining stationary. There was no significant difference in the birds' direction of movement before compared to during the playback (Mann Whitney U test: W=168.0, n=13, p=0.69). There was also no difference between the movement during and after the playback (W=164.5, n=13, p=0.59).

Reaction to different playback types

The difference in rate of species-specific call before and during the playback was calculated in order to determine whether the birds' responses varied depending on the playback type. The change in rate was then log transformed and used as the response variable in a GLM to test how much variation can be explained by playback type. Species-specific vocalisation did not differ in response to any of the playback types ($F_{2,10}$=1.14, p=0.357). A second GLM test was carried out using the data on movement during playback (approach/retreat/remain) as the response variable to determine whether this was affected by the type of playback. Again, there was no significant main effect; movement relative to the speakers is not affected by playback type ($F_{2,10}$=0.77, p=0.489).

Discussion

There was no indication that the spotted bowerbirds in this experiment attended to, or responded to, playback of species-specific calls, mimetic calls or control noise. The birds neither mimicked nor produced species-specific vocalisation in response to playbacks, nor did they move toward or away from the speaker. There was no evidence that birds varied in their response to the different playbacks but this may have been due to the very small sample sizes in each category.

There are several possible reasons for the apparent lack of response to playbacks. Firstly, the playbacks may not have been loud enough to attract the birds' attention. Despite playing the calls at the speakers' maximum volume, it was not possible for the human observers to hear the playbacks from the 20m that separated them. This is in sharp contrast to the bowerbirds' calls, which were easily heard from over 30m and, in good conditions, can be recognised from as far away as 1km (J.R. Madden pers comms). Secondly, the quality of the playbacks may not have been sufficient to deceive the bowerbird. The lack of detectable response means I am unable to determine whether this was an issue in this experiment.

There are also plausible biological reasons for the apparent absence of response. The bowerbirds may be able to distinguish among the different types of call but react the same to them; this reaction could be to continue with the same behaviour. McGregor (2000) described this as the floor effect – the birds perceive the stimuli but respond at a uniformly low level. It is also conceivable that sound recordings alone were not a sufficiently realistic stimulus. Possibly combining the playbacks with a visual cue, like a stuffed bowerbird would have been more successful. Finally, the birds may not be able to detect the differences between the call types, even in natural occurrences.

4.5 General Discussion

The data from these experiments gives mixed support for the Batesian mimicry hypothesis. Whilst the disturbance experiment suggested that mimicry could be involved in threat avoidance, at least in some birds, there was no suggestion that mimicry was used in response to a mount of a bowerbird predator (a falcon). The playback experiment was unable to show whether mimicry had an intraspecific function, although there were severe shortcomings in the experimental protocol, and in the equipment, so the possibility cannot be excluded. Evidence for the function of species–specific hisses is also mixed. Species-specific vocalisation tended to increase in the presence of the falcon but did not vary in response to the human disturbance. These contrasting results could perhaps be due to differing perceptions of threat in the two experiments.

Chapter 5: Individual variation in vocalisation

5.1 Individual variation in rate of species-specific vocalisation

Species-specific vocalisation functions predominantly to attract mates and/or to defend territory from rivals (Catchpole & Slater, 1995). Individual variation in vocal traits can exist in a variety of forms. For example, species-specific repertoire size, a measure of the complexity of song, varies among individuals and correlates with mating success (e.g. in starlings *Sturnus vulgaris*, Mountjoy & Lemon, 1996; Eens, 1997). Similarly the performance of species-specific songs can influence attractiveness and competitive ability: female swamp sparrows (*Melospiza georgiana*) prefer males with the highest trill rate (Ballentine et al., 2004); the strophe length of great tits (*Parus major*) is positively correlated with male dominance at feeding sites (Lambrechts & Dhondt, 1986) and variation in modulation of the "perch-coo" in collared doves (*Streptopelia decaocto*) influences male-male competition (ten Cate et al., 2002).

Spotted bowerbirds are highly vocal birds, especially during their displays at bowers to visiting females and rival males. The vast majority of their vocalisation consists of species-specific hisses, interspersed with occasional mechanical noises and mimicry (see 2.12). From data presented in previous chapters (3 and 4) it appears that the hiss vocalisation in spotted bowerbirds is primarily involved in intraspecific interactions: it potentially increased in the presence of conspecifics and did not change from a basal rate during the simulated disturbance at the bower. Furthermore, Borgia and Presgraves (1998) showed a correlation between the ratio of long to short hisses and mating success, suggesting that properties of the hiss might be sexually selected. I, therefore, suggest that information about an individual's status, age and quality may be ascertained from the rate of species-specific vocalisation. Here, I look at whether individual variation in rate of hiss calls varies with status (bower owner, auxiliary and unknown) and duration of bower tenure, to see if it could provide reliable cues, for instance to visiting females or rival males.

Methods

As described previously (sections 2.13) the rate of species-specific vocalisation was calculated from recordings of both experiments and observations. Data from these are pooled, across years, for the following analyses. Status and tenure duration are defined in sections 2.8 and 2.9 respectively.

Statistical analyses

General linear models and Pearson correlations were used to analyse the data as described in section 2.15. In addition, a repeatability analysis was carried out to see if individual bowerbirds always have a similar rate of species-specific vocalisation. To do this a one-way ANOVA was performed with vocal rate as response and individual as factor. This gives the mean squares for the error and the subject (i.e. individuals), which can be used to calculate Sa, an estimate of the difference between individuals, and Se the error mean square:

Sa = (Subject MS – Error MS)/n   where n= the number of measurements per individual

To calculate n where sample sizes are not equal, as is the case here, the following formula is used (see Lessels & Boag, 1987):

$$n=[1/(a-1)][\sum_{i=1}^{a} n_i-(\sum_{i=1}^{a} n_i^2/\sum_{i=1}^{a} n_i)]$$

where *a* is the number of individuals, n_i is the sample size for the *i*th individual

Se = Error mean square

Repeatability = Sa/(Sa + Se)

Hence, when measurements on the same individual are very consistent, Se is close to zero and the repeatability measure is close to one, indicating near perfect repeatability. If measurements on the same individual are as different as the measurements on different individuals the repeatability is low (close to zero).

Results

The rate of species-specific hiss vocalisation is very variable, both within and between individuals (mean ± SD= 10.17 ±4.76 calls/min, range = 1 - 71 calls/min, see table 5.1 and fig 5.1). A GLM on all the pooled data from experiments and observations showed a significant effect of individual bower owner on the rate of species-specific vocalisation ($F_{20,1410}=8.61$, $p<0.001$) but there was no main effect of experimental treatment (i.e. observations, presentation experiment or disturbance experiment: $F_{2,1410}=1.59$, $p=0.204$). The interaction between experimental treatment and individual could not be tested due to missing data, it is therefore assumed to be zero.

Page ref	Observation/Experiment	F statistic	p value
63	Observation - presence of competitors	$F_{17,4}=1.01$	0.560
64	Observation - presence of aggressive species	$F_{17,7}=3.71$	0.042
65	Observation - presence of conspecifics	$F_{31,24}=1.44$	0.181
70	Observation - seasonal variation	$F_{21,20}=1.43$	0.216
84	Presentation experiment	$F_{12,23}=3.76$	0.003
91	Disturbance experiment - first disturbance	$F_{16,54}=1.90$	0.041
94	Disturbance experiment - all disturbances	$F_{16,55}=2.86$	0.002

Table 5.1: Summary of results from previous chapters showing frequent significant differences in individual species-specific rate

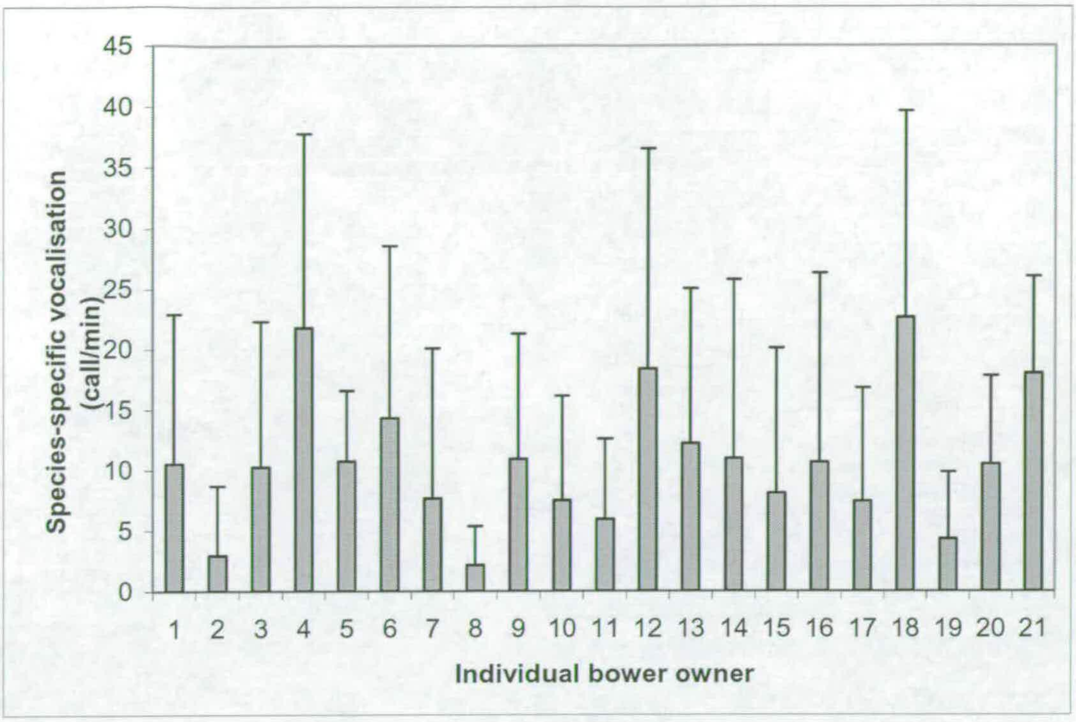


Fig 5.1: Variation in individual rate of species-specific vocalisation of 21 ringed bower owners. Bars show average rate (call/min) ± SD (NB the order of individuals is the same throughout this chapter. They run approximately from the longest known bower owners (1 to 4) through to individuals that have been owners for a minimum of one year (17 to 21) for full details see Appendix A.7).

Variation in rate also occurred within individuals. Males were not always consistent in their rate of species-specific vocalisation – a male with a high species-specific call rate in one experiment did not necessarily show a high rate in others. Although there was a positive correlation between the individual species-specific rate in observations and the presentation experiment (Pearson correlation: 0.615, d.f.=16, p=0.025, fig 5.2 (NB not all bower owners could be included in this analysis as they were not all studied for all experiments), there was no relationship between the individual rate of species-specific vocalisation in the disturbance experiment and either the presentation experiment or the observational data (Pearson correlation: 0.211-0.334, d.f.=16, p>0.3). A repeatability analysis confirms that repeatability of the species-specific vocalisation rate is low within an individual (R= 0.297).

Therefore, within-individual vocalisation rates are almost as variable as the vocalisation rates across all bower owners.

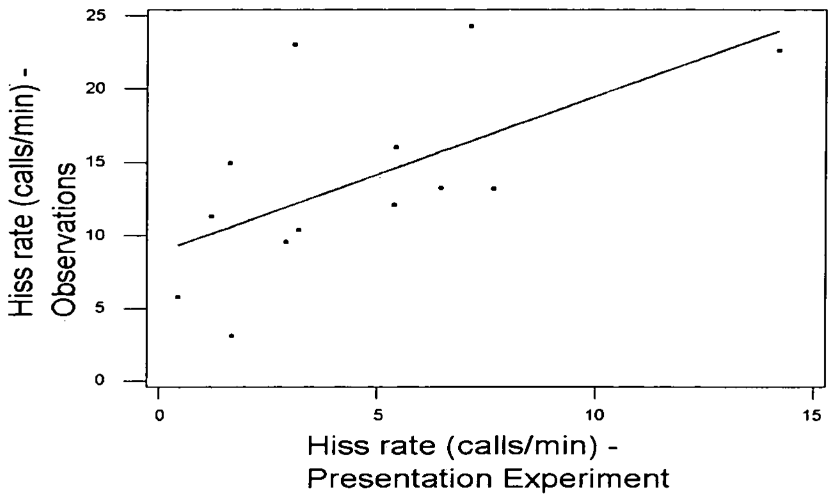


Fig 5.2: Correlation between individual species-specific hiss rate in the presentation experiment versus hiss rate during observations

Status and individual variation in species-specific vocalisation

There was a significant effect of the status (owner or auxiliary, see 2.8) of individual bowerbirds on the rate of species-specific vocalisation (GLM: individual, random factor $F_{27,1951}=8.40$, $p<0.001$, status: $F_{1,27}=6.46$, $p=0.015$). Auxiliaries had a rate of species-specific vocalisation almost two times higher than bower owners (see fig 5.3)

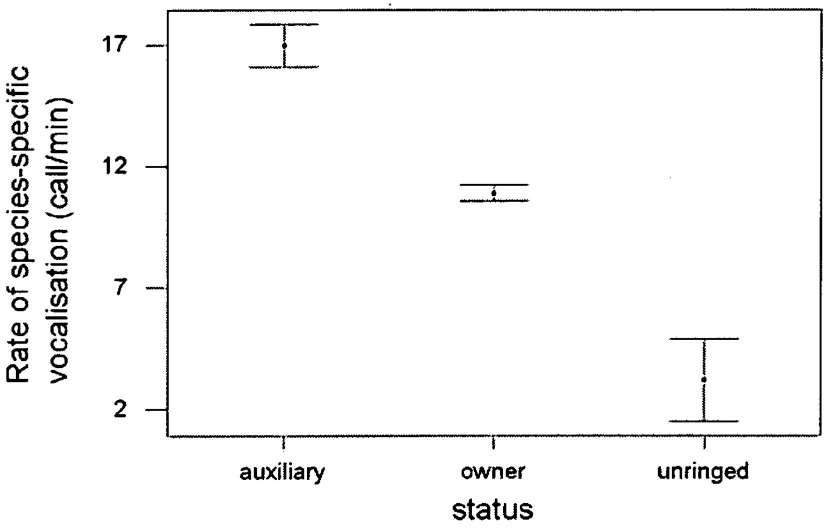
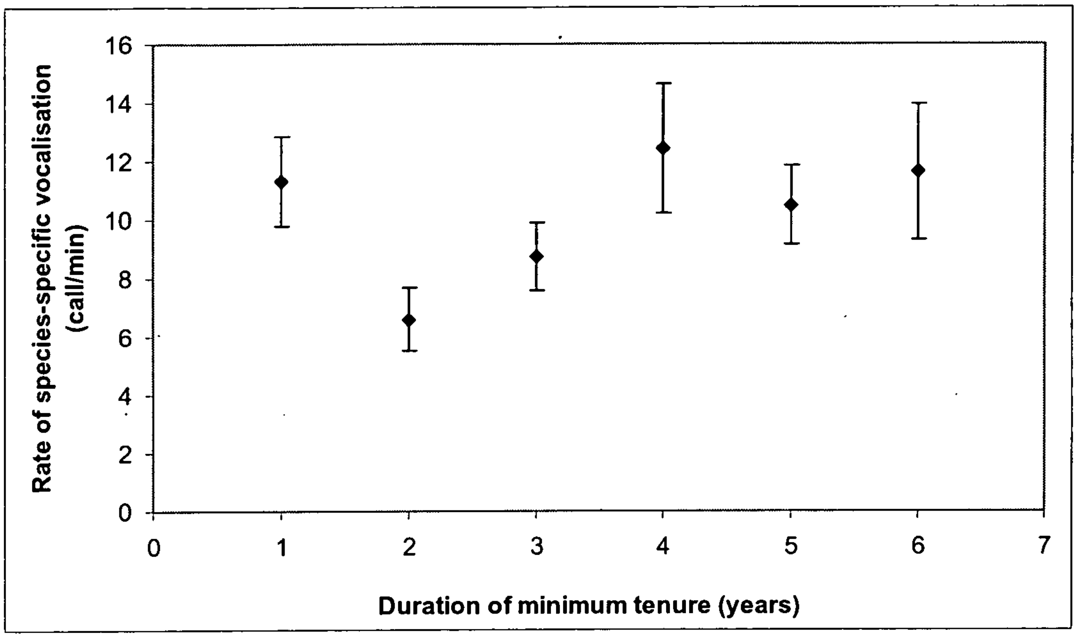


Fig 5.3: Rate of species-specific vocalisation and bowerbird status. Points are calls/min, mean ± SE. Auxiliaries (number of individuals = 8, number of observations = 300, range of call rate = 4 - 67), bower owners (number of individuals = 21, number of observations = 1692, range of call rate = 1-56) and unringed birds (number of observations = 32, range of call rate = 1 – 47).

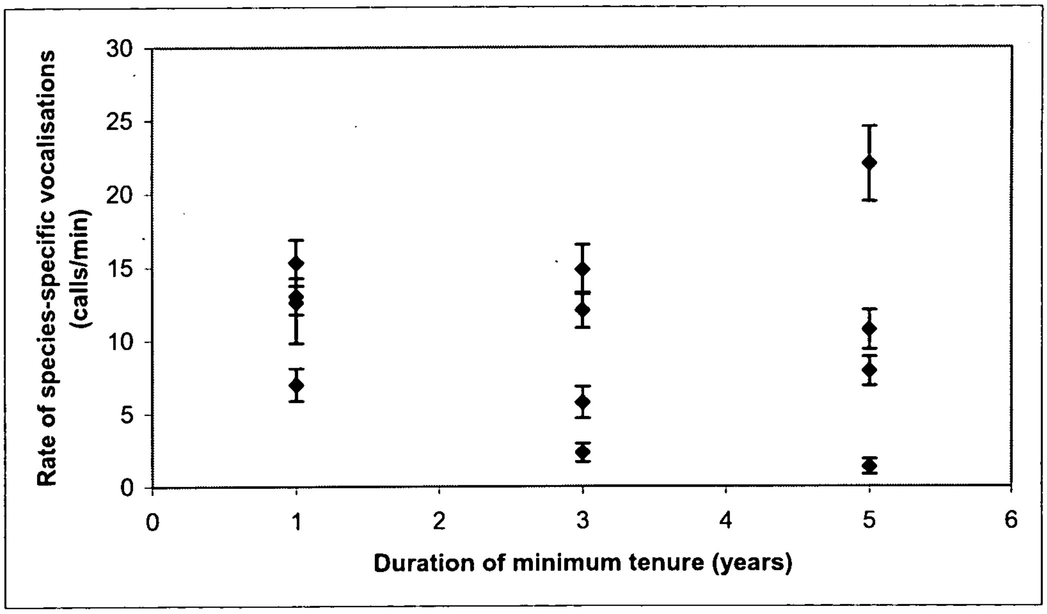
Unringed birds have a lower rate of species-specific vocalisation on average than ringed auxiliaries or owners (GLM: status: $F_{2,27}=3.45$, $p=0.043$, see fig 5.3). Obviously it is not possible to recognise unringed individuals and nothing is known of their status. They could be immature birds, females, owners or auxiliaries at other bowers. It is also impossible to know how many unringed individuals were observed.

Length of tenure and individual variation in species-specific vocalisation

Species-specific vocalisation is affected by both individual identity (GLM: $F_{20,1666}=10.0$, $p<0.001$) and duration of tenure (minimum tenure (co-variate): $F_{1,1666}=6.83$, $p=0.009$). However as figure 5.4 shows there is no clear pattern to this variation. A paired t-test showed there was no tendency for the species-specific rate of individuals to change over the two years of study (t = -0.17, d.f.=15 p = 0.868).



a)



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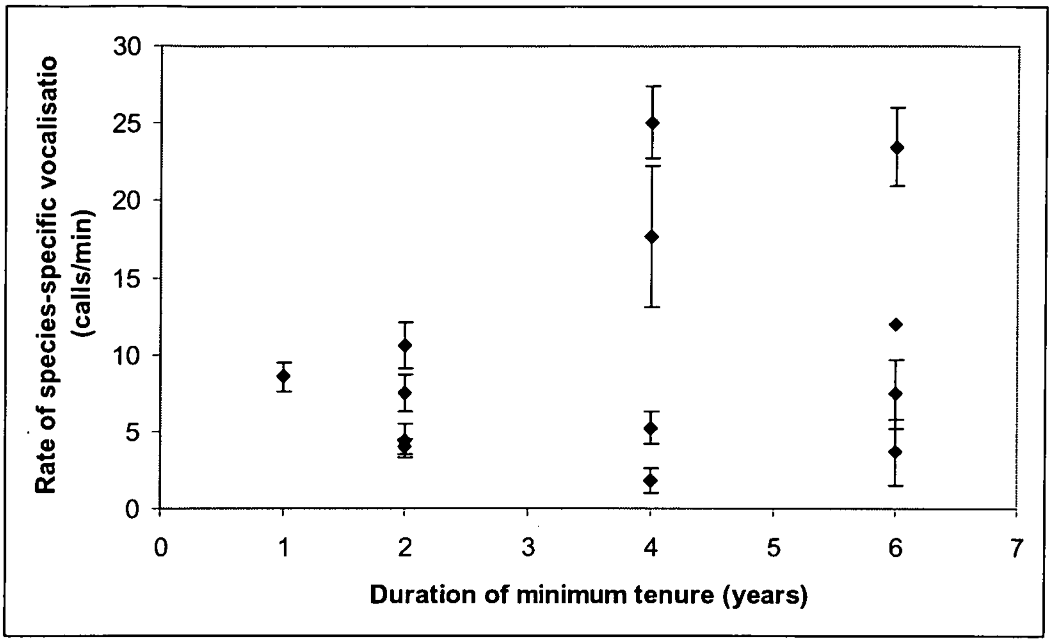


c)

Fig 5.4: a-c) The relationship between the rate of species-specific vocalisation and minimum length of tenure a) for all bower owners (n=21) b) mean rate for all bower owners in 2002 (n=14) c) mean rate for all bower owners in 2003 (n=19). Points are means ± SE

The analysis was repeated using only the ten individuals whose duration of bower ownership was accurately known (i.e. those who were owners all six years this population has been studied, considered to be the maximum length of bower ownership (2.9) or those that have taken over as owner at a bower during the study). The duration of tenure and individual are still significant main effects (GLM individual: $F_{9,646}=16.83$, $p<0.001$, known tenure (co-variate): $F_{1,646}=41.08$, $p<0.001$) but the pattern is no clearer (see fig 5.5). There is a tendency for the highest rates of vocalisation to be found in individuals with the longest tenure, but there is considerable variation within each tenure group. However, as above there was no tendency among this subset of bower owners for the rate of individual species-specific vocalisation to change over the two years (t=-0.38, d.f.=6, p=0.716)

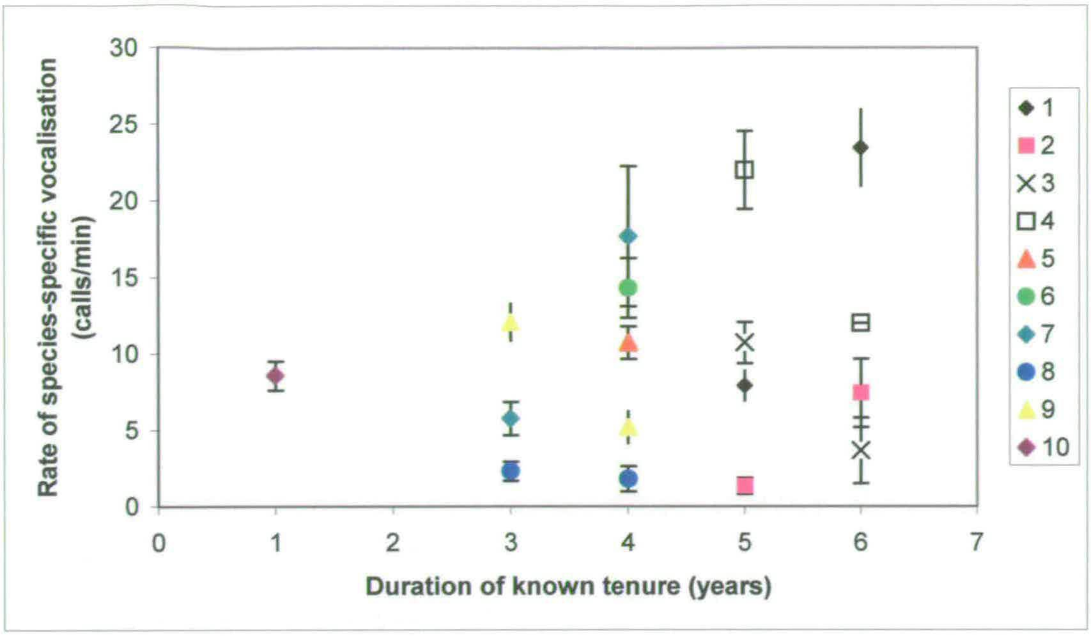


Fig 5.5: Individual rate of species-specific vocalisation (mean ± SE) for bower owners (n=10) against known bower tenure. Bower owners 5 and 6 were only observed in one year of the current study and 10 was a new bower owner in 2003.

Discussion

It is clear that individual spotted bowerbirds do vary in their rate of species-specific vocalisation both within and among individuals and this variation appears to be large enough that it could be biologically significant. Individuals vary in their species-specific rate among the different experimental procedures and in observations. The rate of vocalisation for each male was similar between the observations and the presentation experiment, which may reflect a general lack of reaction to the models (see chapter 4). The lack of similarity in individuals' species-specific vocalisation in the other experiments was confirmed by the repeatability analysis: there is considerable within individual variation. The variation in species-specific rate might be used as a signal, for instance of male quality, but the lack of consistency within an individual would seem to limit its usefulness. The lack of repeatability also implies low heritability (Michalak, 1996).

Species-specific vocalisation rate is correlated with bowerbird status. Auxiliaries have a higher rate of vocalisation than bower owners. Borgia and Presgraves (1998) observed that species-specific vocalisation in spotted bowerbirds, specifically the ratio of long to short hisses is correlated with mating success. It is possible the rate of vocalisation influences mating success too, more successful males possibly hissing at a lower rate but with longer hisses. Unringed individuals called at a lower rate than either auxiliaries or owners. This group encompasses females, non-bower owning males and potentially (although less likely) owners and auxiliaries from unknown bowers. It is perhaps not surprising that the rate of species-specific vocalisation is not only lower than that of owners or auxiliaries but is also more variable. I am not aware of any published data on the rate of female species-specific vocalisation, but it is perhaps likely to be lower than that of males who are very vocal during bower displays.

Hiss rate also appeared to vary with duration of bower ownership. Although it appears that some of the most long-term bower owners may have an elevated call rate, it is not true of all of them. In addition, there was no indication that the vocalisation rate of individuals changed in a predictable way over the two years of the study. It is not obvious why more long-term bower owners would be more similar to auxiliaries in their rate of calling.

There are several limitations in the data. Firstly, there is only a very small sample size of owners for whom the duration of tenure is known. For the remainder it is not known how long they might have been owners for prior to discovery. Secondly, no data were collected in 2001, although it does seem unlikely that owners in 2000 and 2002 would cease to be owners for just this year.

It is still possible, then, that variation in species-specific vocalisation could be used to indicate status or even tenure at bower. To confirm this, longer term data on individuals combined with greater knowledge of the function of the species-specific vocalisation would be required. In particular it might be important to consider the rate of vocalisation specifically during displays to conspecifics at the bower separately from its use at other times. It would also be useful to measure the rate of species-specific vocalisation and mating success in the same individuals to demonstrate whether there is a relationship.

5.2 Estimation of repertoire size

Repertoire size is one measure of the complexity of an individual's or a species' song. Repertoire size has been correlated with various life history traits in many studies. For example, males with larger repertoires pair earlier (Howard, 1974; Catchpole, 1980; Eens et al., 1991), have larger and better quality territories (McGregor et al., 1981; Hiebert et al., 1989), more mates (Eens at al , 1991), more extra-pair copulations (Hasselquist et al., 1996) and greater lifetime reproductive success (Hiebert et al., 1989). Such inter-individual comparison requires an estimate of complete repertoire size and there is on-going debate about the best way calculate this (Catchpole & Slater, 1995; Garamszegi et al., 2002; Garamszegi et al., 2005). Traditionally, repertoire size has been estimated from the asymptote of a cumulative plot (e.g. Wildenthal, 1965), more recently capture-recapture models have been used (Garamszegi et al., 2002).

All of the above studies involve *species-specific* vocalisation in territory defence or mate attraction. Estimation of *mimetic* repertoire sizes has received much less attention, and none at all with regard to the proposed function of threat avoidance. Some studies (e.g. Dowsett-Lemaire, 1979; Hindmarsh, 1984) assume full mimetic repertoires are captured from sufficiently long recordings. Hamao and Eda-Fujiwara (2004) recorded 250 syllable switches in the black-browed reed warbler (*Acrocephalus bistrigiceps*) as previous studies suggested this was sufficient to capture most song types. They then used Principle Component Analysis (PCA) to determine whether putative mimetic vocalisations (identified by visual inspections of sonograms) were acoustically similar to model calls. Many calls that were suspected to be mimicry were judged not to be using this technique. They found that mimetic repertoire did not correlate with pairing date, but conceded that the relationship could have been obscured due to the PCA procedure underestimating individual repertoires. They did not allow for the possibility that not all mimicry types were recorded. Although Howard (1974) used asymptotes to estimate the repertoire size, including mimicry, of mockingbirds (*Mimus polyglottos*), I am not aware of any study in which estimation methods normally used on species-specific repertoires, have been used to estimate only the *mimetic* repertoire size.

Traditionally, estimates of repertoire size have been derived from a cumulative plot of the number of song units recorded against the number of unique types of song units (e.g. Eens et al., 1991; Catchpole and Slater, 1995, fig 5.6). The point at which this plot forms an asymptote represents the number of song units in the individual's or population's repertoire. Alternatively a formula, based on the shape of the asymptotic curve can be used to predict repertoire size (Wildenthal, 1965; Howard 1974). These approaches have been criticised for not allowing for the heterogeneity of use of different song types (Garamszegi et al., 2002). For example, some types of song unit are sung frequently whilst others are more rare. It is obvious that rarer songs are less likely to be detected during necessarily limited recordings. More recently, species richness estimations from community ecology have been applied to the estimation of repertoire size (Garamszegi et al., 2002, 2005). These capture-recapture models have the advantage of allowing for the heterogeneity of detection of different song types. To date, no one has estimated mimetic repertoire size using these capture-recapture techniques.

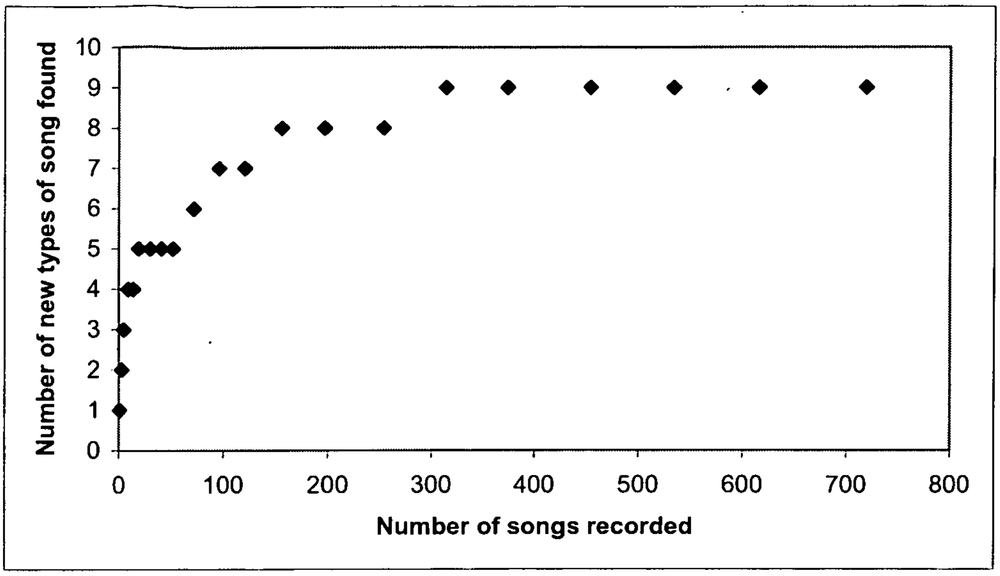


Fig 5.6: Example of a cumulative plot for showing the increase in number of new songs recorded as the total number of songs recorded increases, until it reaches an asymptote at 9, the estimated repertoire size of this individual (12).

One potential confounding factor in the observed repertoire size is that individuals that have been recorded for longer periods will appear to have larger mimetic repertoire sizes purely because there is a greater chance of capturing different and rare types of mimicry. Although estimation techniques account for this to some extent, it may affect the accuracy of the estimate. In particular, the length of time of recordings could account for differences between the two years. In 2002 only 14 bowers were studied compared to 20 in 2003 and consequently the average length of observations in 2003 were shorter (see 2.10 for details).

I use both traditional asymptotic and capture-recapture techniques to estimate the mimetic repertoire size in individual spotted bowerbirds and within the population studied at Taunton. I then compare the repertoire size to the time spent recording at each bower and the proportion of time the owner was present to check whether these were indeed confounding factors.

Method

I recorded vocalisation from 21 bower owners and three auxiliary birds. While other birds were recorded mimicking, they are not included in the following analyses as either they could not be identified or were only heard on a very few occasions. I took a mimetic bout to be mimetic calls which were uninterrupted by species-specific hisses. Within that bout, mimicry can be broken up into units according to the type of mimicry. For the purposes of estimating repertoire size the type of mimicry is defined as mimicry of any one model. Hence, although I could subdivide the whistling kite mimicry into the descending whistle and the si-si-si components (which can sometimes be heard separately (Simpson & Day, 1999)) here I consider them as just one type of mimicry. The total number of these different types of mimicry recorded gives the observed repertoire size. The number of different types of mimicry and their occurrence within bouts were used in the two techniques for estimation of repertoire size described below.

1) Asymptotic technique

The curve obtained by plotting the number of new mimetic (song) types against the total number of mimetic (song) bouts is approximated by the following equation (see fig 5.6, Howard, 1974):

$$n=N(1-e^{-T/N})$$

where n is the number of unique mimicry types detected in the sample (the observed repertoire size), T is the total number of mimetic bouts in the sample and e is the exponential constant (2.718). N represents the total number of mimicry types in the complete repertoire. The value of N is estimated by choosing a value for it ($N=n$, $N=n+1$ etc) and solving the equation for n. This is repeated until the value calculated for n is equal to the expected number (i.e. the number of different mimicry types detected), this value of N gives the estimation of the complete repertoire size.

This technique was used to estimate individual repertoire size as well as the complete repertoire size of this population of bowerbirds over the two years.

2) Capture-recapture technique

The second method of repertoire size estimation, based on the "capture-recapture" model, was carried out using the software Comdyn (Garamszegi et al., 2002, http://www.mbr-pwrc.usgs.gov/software/specrich2.html). The presence or absence of each mimetic type was recorded for each male (see table 5.2). The variables n_h (the number of mimicry types in each mimetic bout) and f_h (the number of types of mimicry encountered in exactly 1, 2, 3 and so on, recording bouts) were the input for the jackknife estimation. Comdyn calculates an estimated repertoire size using the following formula:

$$\tilde{N} = R + \sum_{h=1}^{K} \alpha_{hk} f_h$$

where R is observed repertoire size, f_h is as above, α_{hk} is a constant generated by the jackknife procedure and K is the total number of songs analysed.

If all the types of mimicry are detected many times (i.e. in nearly all mimetic bouts) the estimated repertoire size is close to the observed one. If, however, many types of mimicry are only encountered in one or two mimetic bouts, it is likely that other types of mimicry have not been observed at all and the jackknife estimate will be greater than the observed repertoire size.

The output from Comdyn gives a jackknife estimate of repertoires size ($\tilde{N} \pm$ SE).

	Bouts of mimicry																						
Types of mimicry	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**Detection occurrence**
apostlebird																						1	1
brown falcon	1	1	1		1					1				1	1		1		1	1	1		11
bush stone curlew		1				1				1	1	1	1			1		1					8
cat			1	1			1	1	1	1	1	1	1			1	1						11
magpie																					1		1
noisy miner																	1						1
n_h	1	2	2	1	1	1	1	1	1	3	2	2	2	1	1	2	3	1	1	1	2	1	
f_h	3	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	

Table 5.2: Example of the presence/absence data used in the jackknife estimation. n_h is the number of different types of mimicry detected in each bout, f_h is the number of types of mimicry detected in 1,2...22 bouts (i.e. in this example, three types of mimicry were detected in only one mimetic bout and none are detected in all 22 bouts). n_h and f_h are the values entered into the Comdyn software.

A chi-squared goodness-of-fit test compares the observed data to expected values from the model, such that $p>0.05$ indicates no significant difference between observed and expected (i.e. the model is a good fit for the data).

For each bower I calculated the duration of recordings. This is equivalent to the effort put into capturing each bower owner's vocalisation, as the recording would be made for a whole observation regardless of whether the owner was present. I also calculated the length of time the bower owner was present within the bower area (defined as within around 20m of the bower) and what proportion of the total observation time they were present. I then looked for correlations between these measures and the observed and the estimated repertoire size. Three auxiliaries were also included in the analysis. Each auxiliary is linked to a particular bower, I measured the proportion of observations that they were present there. I calculated mean individual rates of vocalisation (mimetic and species-specific – See section 2.13) and looked for a relationship to proportion of time spent at the bower.

Results

1) Asymptotic technique

The estimated population repertoire size was 16, the same as the detected repertoire size. Table 5.3 shows the estimated individual repertoire sizes using this method. In just one out of 42 cases the estimation is the same as the detected repertoire size (shown in bold). In all other cases the estimated repertoire size was larger than the detected repertoire size. In 26 instances the estimated repertoire size was within the limit of the population repertoire size (i.e. <16), but in the remainder the estimated repertoire size was larger than detected for any individual or the estimation of the population repertoire size (i.e. >16). In 12 cases the estimated size was over 100. The average estimated repertoire size (not including estimated repertoires of over 100) was 9.89 in 2002, 8.36 in 2003 and 12.22 in both years combined. If all estimates are included (those of 100+ are capped at 100) the average repertoire sizes are 52.29, 28.00 and 28.18 for 2002, 2003 and both years respectively. These are considerably larger than the observed average repertoire sizes of 5.18, 4.05 and 7.91 (see also table 5.3 and fig 5.7).

Bowerbird ID	2002				2003				Both years			
	n	*T*	*N*	difference	*n*	*T*	*N*	difference	*n*	*T*	*N*	difference
1	5	11	6	1	3	4	7	4	6	15	7	1
2	5	6	15	10	0	0	*	*	*	*	*	*
3	13	25	17	4	6	16	7	1	14	41	15	1
4	5	8	8	3	1	*	*	*	6	9	10	4
5	*	*	*	*	**6**	**22**	**6**	**0**	*	*	*	*
6	5	7	10	5	*	*	*	*	*	*	*	*
7	3	4	7	4	*	*	*	*	*	*	*	*
8	2	2	100+	*	1	*	*	*	3	3	100+	*
9	3	5	4	1	1	*	*	*	3	6	4	1
10	3	3	100+	*	7	14	9	2	7	17	8	1
11	2	2	100+	*	*	*	*	*	*	*	*	*
12	9	8	100+	*	3	3	100+	*	11	11	100+	
13	6	6	100+	*	5	12	6	1	9	18	11	2
14	6	4	100+	*	6	10	9	3	8	14	11	3
15	3	3	100+	*	5	6	15	10	8	9	29	21
16	12	24	15	3	6	5	100+	*	12	29	15	3
17	*	*	*	*	8	18	9	1	*	*	*	*
18	*	*	*	*	3	7	4	1	*	*	*	*
19	*	*	*	*	2	1	*	*	*	*	*	*
20	*	*	*	*	6	9	10	4	*	*	*	*
21	*	*	*	*	5	7	10	5	*	*	*	*
22	4	6	7	3	*	*	*	*	*	*	*	*
23	*	*	*	*	3	3	100+	*	*	*	*	*
24	2	2	100+	*	*	*	*	*	*	*	*	*
AVERAGE	5.18		9.89	3.78	4.05		8.36	2.91	7.91		12.22	4.11
SD	3.30218288		4.64878		2.344584403		2.9077		3.47719845		7.2246	

Table 5.3: Estimated repertoire size (*N*) using asymptotic technique. “Difference” refers to the difference between the estimated and detected repertoire size for individual bowerbirds (*n* = detected repertoire size, *T* = total number of mimetic bouts, *N* = estimated repertoire size). There are missing values for many birds, this may be because the bower was not detected in one year, the bird was not observed or there were no recordings of the individual’s mimicry. Bowerbirds 18, 19 and 21 were only banded during the 2003 field season. Averages do not include estimates over 100, see text.

2) Capture-recapture technique

It was not possible to estimate a population repertoire size using the Comdyn software, simply because the number of mimetic bouts recorded exceeded the number of columns the software allows. This problem was not encountered when estimating individual repertoires. The estimates of individual repertoire size using this technique are summarised in table 5.4 and fig 5.8. The estimated repertoire was the same as the detected in eleven out of 42 cases (shown in bold), greater but within the estimated population repertoire (i.e. <16, see above) in 27 cases and greater than the population repertoire size in four instances. The goodness-of-fit tests for the model (M_h) had $p>0.05$ in all but one instance (starred in table 5.4), indicating the model was a good fit for the observed data. The mean estimated repertoire size was 7.29 in 2002, 7.36 in 2003 and 10.90 in both years combined.

Both methods of estimating repertoire size gave results that were significantly higher than the detected repertoire size (see table 5.5, fig 5.7 and 5.8, paired t-tests: t=-2.28—5.42, d.f. = 9-18, p= 0.001- 0.039). There was no difference between the estimated repertoire sizes using the two techniques, if values greater than 100 were removed (paired t-tests: t=-0.43-0.33, d.f.=9-12, p=0.679-0.790). Even including these large estimates, there was only a significant difference between asymptotic and capture-recapture estimates in 2002 (paired t-test: t=3.82, d.f. = 17, p=0.001) with the asymptotic values being greater.

	2002						2003						both years					
Bowerbird ID	**n**	$\tilde{N}$	**SE**	**chi sq**	**df**	**p**	**n**	$\tilde{N}$	**SE**	**chi sq**	**df**	**p**	**n**	$\tilde{N}$	**SE**	**chi sq**	**df**	**p**
1	5	11	4.586	1.136	10	0.997	3	5	2.204	1	3	0.801	6	12	4.316	1.978	14	0.999
2	**5**	**5**	2.346	3.125	5	0.681	0	*	*	*	*	*	*	*	*	*	*	*
3	13	15	3.489	23.946	24	0.465	6	7	1.998	2.854	15	1	14	15	4.497	31.822	40	0.818
4	5	17	7.2	6.2	7	0.5166	1	*	*	*	*	*	6	22	8.507	5.333	8	0.721
5	*	*	*	*	*	*	6	17	10.525	10.525	21	0.971	*	*	*	*	*	*
6	5	6	1.852	0.857	6	0.991	*	*	*	*	*	*	*	*	*	*	*	*
7	3	4	1.67	0	3	1	*	*	*	*	*	*	*	*	*	*	*	*
8	2	3	1.225	0	1	0	1	*	*	*	*	*	3	5	2.449	1	2	0.607
9	**3**	**3**	1.249	6	4	0.199	1	*	*	*	*	*	3	3	1.292	7.857	5	0.164
10	3	5	2.449	0	2	1	**7**	**7**	2.435	2.628	13	0.999	7	7	2.523	2.736	16	0.9999
11	2	3	1.225	0	1	1	*	*	*	*	*	*	*	*	*	*	*	*
12	9	11	3.001	6.186	7	0.5182	3	5	2.449	0	2	1	11	14	3.397	7.564	10	0.671
13	6	7	1.828	9.524	5	0.0899	5	6	1.969	4.965	11	0.9329	9	11	2.464	16.569	17	0.482
14	**6**	**6**	1.348	9	3	**0.0293***	**6**	**6**	2.456	4.451	9	0.879	**8**	**8**	9.706	8.991	13	0.774
15	3	4	1.521	0.667	2	0.717	**5**	**5**	2.346	1.25	5	0.94	8	10	3.363	1.674	8	0.894
16	12	16	4.347	5.147	23	1	**6**	**6**	3.389	0.667	4	0.9554	12	13	2.938	5.877	28	1
17	*	*	*	*	*	*	**8**	**8**	1.423	20.113	17	0.269	*	*	*	*	*	*
18	*	*	*	*	*	*	**3**	**3**	1.371	2.143	6	0.906	*	*	*	*	*	*
19	*	*	*	*	*	*	2	*	*	*	*	*	*	*	*	*	*	*
20	*	*	*	*	*	*	**6**	**6**	2.439	1.895	8	0.9841	*	*	*	*	*	*
21	*	*	*	*	*	*	5	17	6.965	0	6	1	*	*	*	*	*	*
22	4	5	1.809	0	5	1	*	*	*	*	*	*	*	*	*	*	*	*
23	*	*	*	*	*	*	3	5	2.449	0	2	1	*	*	*	*	*	*
24	2	3	1.224	0	1	1	*	*	*	*	*	*	*	*	*	*	*	*
Average	5.17647	7.29412					4.05263	7.35714					7.90909	10.9091				

Table 5.4: Estimated repertoire size ($\tilde{N}$) using capture-recapture jackknife model. (n = detected repertoire size, $\tilde{N}$ = estimated repertoire size, p = probability of goodness of fit test) There are missing values for many birds, this may be because the bower was not detected in one year, the bird was not observed or there were no recordings of the individual's mimicry. Bowerbirds 18, 19 and 21 were only ringed during the 2003 field season. Some sample sizes were too small to calculate jackknife estimates of repertoire size.

	2002			2003			Both years		
Bowerbird ID	n	N	Ñ	n	N	Ñ	n	N	Ñ
1	5	6	11	3	7	5	6	7	12
2	5	15	5	0	*	*	*	*	*
3	13	17	15	6	7	7	14	15	15
4	5	8	17	1	*	*	6	10	22
5	*	*	*	6	6	17	*	*	*
6	5	10	6	*	*	*	*	*	*
7	3	7	4	*	*	*	*	*	*
8	2	100+	3	1	*	*	3	100+	5
9	3	4	3	1	*	*	3	4	3
10	3	100+	5	7	9	7	7	8	7
11	2	100+	3	*	*	*	*	*	*
12	9	100+	11	3	100+	5	11	100+	14
13	6	100+	7	5	6	6	9	11	11
14	6	100+	6	6	9	6	8	11	8
15	3	100+	4	5	15	5	8	29	10
16	12	15	16	6	100+	6	12	15	13
17	*	*	*	8	9	8	*	*	*
18	*	*	*	3	4	3	*	*	*
19	*	*	*	2			*	*	*
20	*	*	*	6	10	6	*	*	*
21	*	*	*	5	10	17	*	*	*
22	4	7	5	*	*	*	*	*	*
23	*	*	*	3	100+	5	*	*	*
24	2	100+	3	*	*	*	*	*	*
average	5.17647	9.88889	7.29412	4.05263	8.36364	7.35714	7.90909	12.222	10.9091

Table 5.5: Summary of observed repertoire size (n), asymptotic estimate of repertoire size (N) and capture-recapture estimate of repertoire size (Ñ) for 24 individual bowerbirds over two years

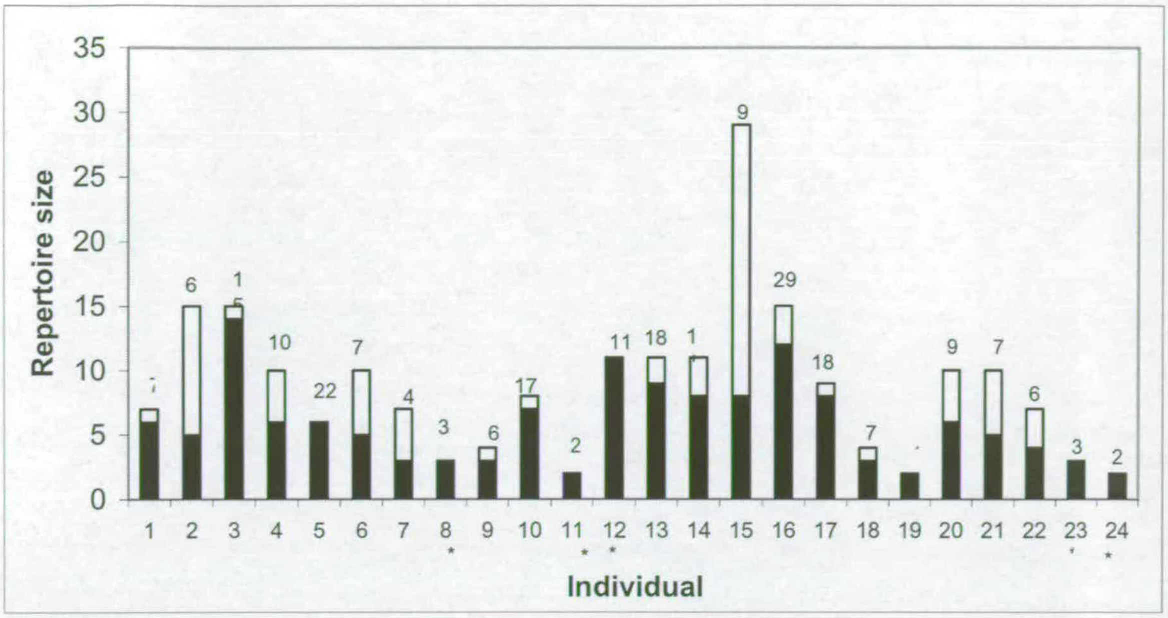


Fig 5.7: Individual observed repertoire size for (black) and asymptotic estimated repertoire size (white and black combined) for both years. The numbers above each bar represent the number of mimetic bouts recorded for that individual. There was no estimation of repertoire size for individual 19 as the sample size was too small. * indicate estimated repertoire sizes of 100+ which are not illustrated on the chart

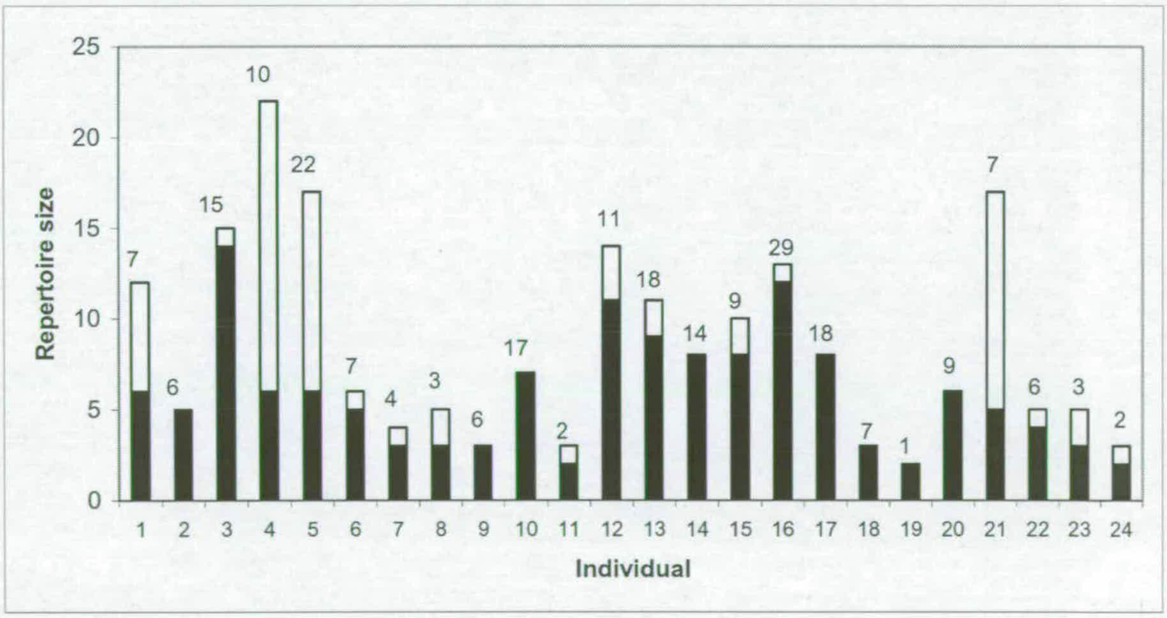


Fig 5.8: Individual observed repertoire size (black) and estimated capture-recapture repertoire size (white and black combined) for both years. The numbers above each bar represent the number of mimetic bouts recorded for that individual. There was no estimation of repertoire size for individual 19 as the sample size was too small.

Individual repertoire size (observed or estimated) was not correlated with the duration of recording at that particular male's bower (Pearson correlation = 0.197, d.f. = 22, p=0.357, estimated: Pearson correlation = -0.151, d.f.=22, p=0.491). However, the observed individual repertoire size was positively correlated with both the absolute length of time the individual was present and the proportion of total observations the individual was present at the bower (Pearson correlation (absolute time present) = 0.771, d.f. = 22, p<0.001 see fig 5.9 and Pearson correlation (proportion of observation present) = 0.737, d.f. = 22, p<0.001). There was no correlation between the estimated repertoire size and the absolute length of time the individual was present, although the trend was also positive (Pearson correlation = 0.306. d.f. =22, p=0.156, see fig 5.10). The proportion of the total observation that an individual was at a bower was positively correlated with estimated repertoire size (Pearson correlation = 0.447, d.f. = 22, p = 0.032).

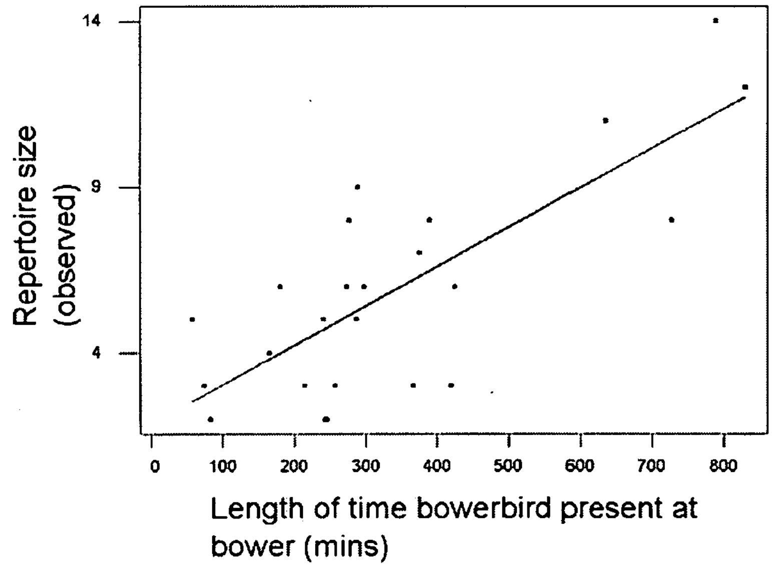


Fig 5.9: Correlation between observed repertoire size and length of time an individual bowerbird is present around the bower (n=24)

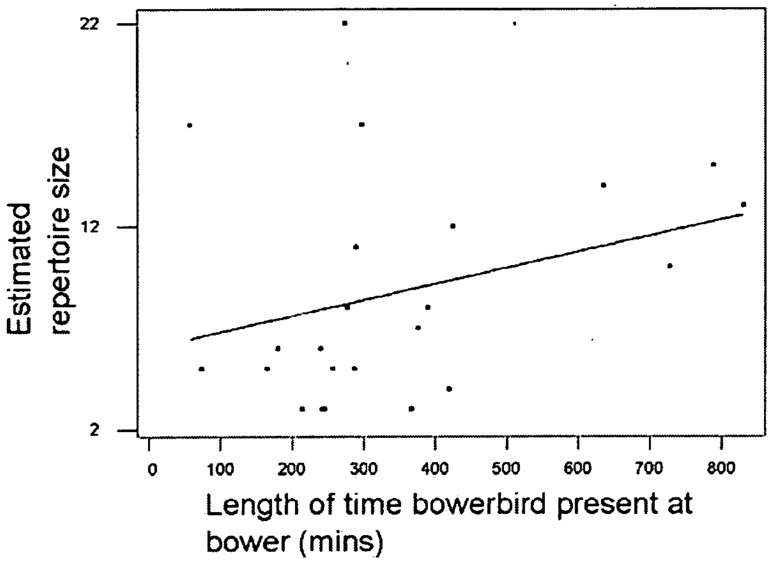


Fig 5.10: Non-significant correlation between estimated repertoire and length of time an individual bowerbird is present around the bower (n = 24)

Discussion

Observed individual repertoire sizes ranged from 2 to 14. Estimated repertoire sizes ranged from 4 to over 100 for the asymptotic technique and between 4 and 22 for the capture-recapture method. Both techniques of estimation suggest that the repertoire size of most individuals is larger than that detected. The asymptotic technique estimated some individual repertoires to be over 100, a value far in excess of that observed in any individual, or of the estimated repertoire size of the population. However, with the exception of these very large estimates, there was no significant difference in the repertoire sizes predicted by this and the capture-recapture technique. The general agreement of the two techniques suggests they both provide a reasonable estimate of complete individual repertoire size.

The estimation (asymptotic) of the population mimetic repertoire size was the same as the observed repertoire size: 16 different model species (limitations in the software used prevented a similar estimation using the capture-recapture technique). This suggests sufficient recordings were made to have captured all the different types of mimicry within the population - a good basis to answer questions about what type of models are mimicked (see chapter 3). However, within the recordings other potentially mimetic vocalisations of unknown models were detected, identification of which could have increased the repertoire size of the population and of individuals. Frith and Frith (2004) name 18 avian and mammalian models as well as five other environmental sounds (like "emus crashing through twanging fence wire"), but this was from a collection of, largely anecdotal, observations from numerous populations. There is no estimate of an individual or population repertoire size, but it appears that my estimate of the population mimetic repertoire is within the range of previously published observations.

Most discussion of repertoire size is confined to species which have large repertoires and/or which sing a lot. Therefore, even with a relatively short amount of recording many bouts can be captured, increasing the likelihood of capturing all different song types. For example, Hiebert et al. (1989) recorded no new song types after just 90 minutes of continuous recordings of male song sparrows (*Melospiza melodia*). By comparison, the mimicry of the spotted bowerbird is sporadic, unpredictable and rare. Accordingly, only a small number of "mimetic bouts" per individual are recorded (i.e. just 11 bouts of mimicry for bowerbird 12, in 635 minutes of recording, compared to 164 species-specific bouts during the same time). Any given type of mimicry is therefore heard very rarely. This leads to the astronomically high estimates of repertoire size using the asymptotic method, as often a new type of mimicry was encountered in every bout. The asymptotic technique predicts that new mimicry types continue to be discovered at this same rate. It seems unlikely an individual will have over 100 mimicry types when the population-wide repertoire size is estimated at 16. The capture-recapture method gives more feasible estimates because it takes into consideration the heterogeneity of use of song types. By including information on the frequency of detection of individual song/mimicry types the estimate is not over-inflated by the detection of a few rare calls.

The estimation of repertoire size is fraught with difficulty and is the subject of ongoing discussion (e.g. Catchpole and Slater, 1995; Garamszegi et al, 2002, 2005). There are both analytical and biological problems. The analytical problems include the ability of each estimation technique to deal with small sample sizes, both in terms of the size of the repertoire and the number of mimetic bouts.

The capture-recapture techniques used were designed for analysis of large population data and should be used with caution with smaller repertoire sizes (Garamszegi et al., 2005). However, for the data tested here the goodness of fit tests were, in the majority of cases, far from significant and the repertoire size estimations were biologically sensible. The limitations of the asymptotic technique were more apparent with very small samples of mimetic bouts, as each bout tended to produce new mimicry types, resulting in unrealistically high estimations (see above). More work is required to establish how applicable existing estimates of repertoire size are to small repertoires of rarely encountered calls, like the mimicry of the spotted bowerbird.

The biological difficulties include defining a mimetic unit and bout and the categorisation of different types of mimicry. These considerations are perhaps more problematic when attempting to find the size of a *mimetic* repertoire, not least because they have not been adequately discussed. I am not aware of any study that has specifically used estimation techniques to predict individual mimetic repertoire sizes.

The initial biological problem is the definition of a biologically significant, and repeatable, unit of song (i.e. syllable, note, song) which makes up the repertoire. I defined such a unit as mimicry of one type of model. Although it is possible to break down mimicry of one model into more than one element (the example of the whistling kite was given earlier), it seems likely that the type of model defines the biologically significant unit. This is especially true if mimicry is involved in threat avoidance as the number of different models mimicked is perhaps more significant than several elements copied from the same model (see chapters 3 and 4)

The definition of a mimetic bout is more troublesome. In a biological sense a bout should perhaps be defined as the length of time the intended receiver is likely to be listening. However, little is known about how repertoires function during the perception of song (Garamszegi et al., 2005), and even less of mimetic vocalisation. Splitting mimetic bouts up by the interruption of species-specific vocalisation, seems to be both a biologically and analytically convenient definition. If, for example, mimicry is serving a predator avoidance function, the "deception" ceases when the bowerbird makes species-specific vocalisation.

Finally, the categorisation into different mimetic types is largely subjective. However, as the inter-observer repeatability tests show (section 2.14), there was a reasonable level of agreement amongst volunteers and myself. Also, as I carried out all of the sound analyses, any idiosyncrasies in categorisation of mimicry would affect all individuals' repertoire sizes to the same extent.

The observed and estimated repertoire sizes are not affected by the recording effort. However, bower owners did vary in the proportion of observation time they spent around the bower and this is positively correlated to both measures of repertoire size. The observed repertoire size is also positively and significantly correlated with the absolute length of time individual birds were present around the bower. Although this relationship is not significant using estimated repertoire size, the trend is in the same direction. This would be expected as the estimation technique should be able to allow for different lengths of observation

It is probable that the complete mimetic repertoire was not captured for each individual and even at the population level I may have recorded, but failed to recognise, different types of mimicry. Although the estimated repertoire sizes may be a more accurate reflection of the true repertoire size, they can tell us nothing about which additional models are mimicked. Therefore in the analyses for rest of the chapter I will use both the capture-recapture estimated repertoire size (from now on just referred to as the estimated repertoire size) and the observed repertoire size. The estimated repertoire size appears to sufficiently address the potential confounding factor of males being recorded for different lengths of time.

5.3 Individual variation in mimetic vocalisation

The importance of individual species-specific repertoire size in mating success in evident (Hiebert et al., 1989; Eens et al., 1991; Hasselquist et al., 1996) but while individual differences in species-specific repertoire size and composition have been well studied far fewer studies have addressed the same questions for mimetic repertoires (e.g. Hindmarsh, 1984; Hamao and Eda-Fujiwara, 2004) In particular, I know of no study that has investigated the size of individuals' mimetic repertoires over the course of their lifetime or whether there is individual variation in rate of mimetic calls.

Previous chapters have shown, there is both inter and intra-individual variation in the rate of mimetic vocalisation in bowerbirds. Some individuals mimic more frequently than others and individual mimetic rate can vary considerably, as seen, for example, in the increase observed during simulated disturbances. Similarly there are individual differences in repertoire size. Here I look at the individual variation in rate and repertoire size in relation to bowerbird status and duration of tenure and also whether the repertoire composition changes over time.

Method

The rate of mimetic vocalisation was recorded for bowerbirds at bowers in a series of experiments and observations as described previously (2.13). Data were pooled from all experiments and observations, except where stated otherwise. The observed and estimated repertoire sizes for 21 ringed bower owners and six ringed auxiliaries were calculated, as described in 5.2. The type of mimicry (i.e. the model) was also noted to compare the composition of individuals' repertoires. The repertoire size and composition were calculated separately for each of the two years.

Results

Individual variation in rate, repertoire size and composition

The rate of mimetic vocalisation is highly variable among and within individuals (mean ± SD=2.23+2.750 calls/min, range = 1 – 103 calls/min, see fig 5.11). Mimetic rate varied among individuals in the disturbance experiment (4.3) and there were significant interactions between individual and treatment (2.15), indicating variation in the use of mimicry among individuals. Using the combined data from all observations and experiments, there was a significant effect of both individual bower owner and experiment on the rate of mimicry (GLM: individual (random): $F_{20,310}=2.72$, $p<0.001$, experiment: $F_{2,310}=37.08$, $p<0.001$).

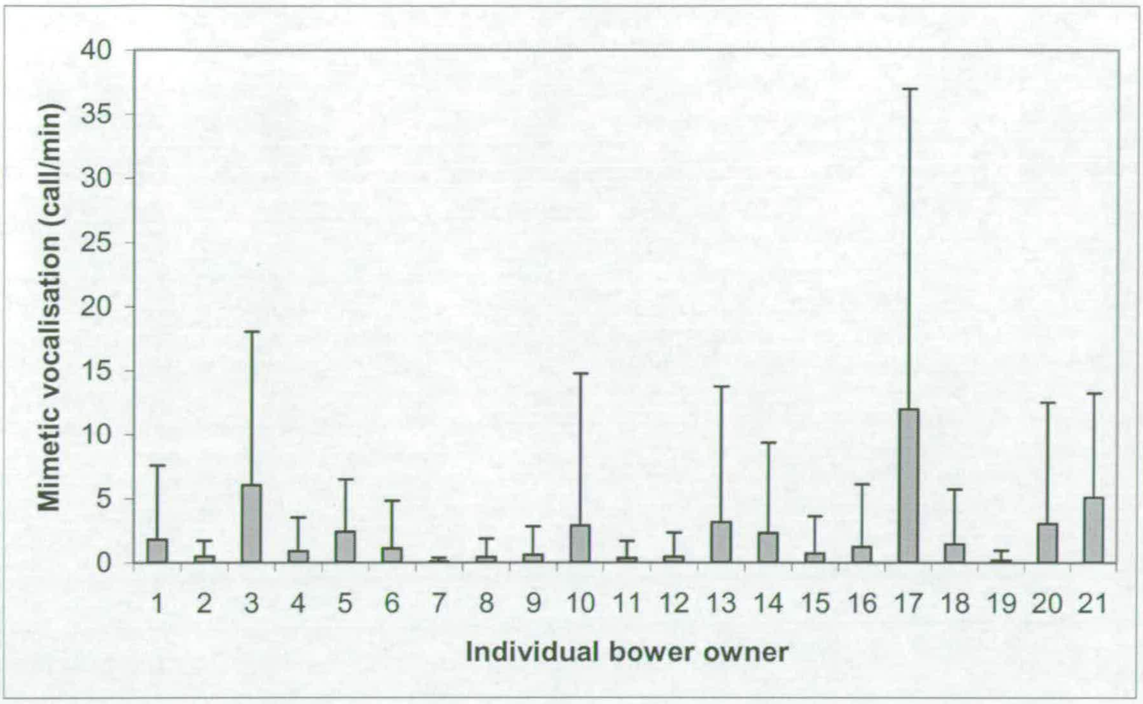


Fig 5.11: Variation in individual rate of mimetic vocalisation of 21 ringed bower owners. Bar shows average rate (call/min) ± SD

The potential for variation in individual mimetic call rate is exemplified by the data from the disturbance experiment. Of the five individuals that mimicked during minute 3 (the time of the disturbance) the mimetic rate was between 4 and 30 times greater than their average observational rate. This increase is marginally non-significant (paired t-test: t=-2.70, p=0.054, n=5).

As with species-specific vocalisation, the individuals with the highest rate of mimetic vocalisation in one experiment were not always more vocal in others. There was no correlation between the individual rate of mimetic vocalisation in the disturbance experiment, presentation experiment or the observations (Pearson correlation: -0.038 – 0.231, d.f.=16, p>0.470, fig 5.12). This is confirmed by a very low individual repeatability score (see section 5.1, R=0.219). As with species-specific vocalisation there is nearly as much variation in mimetic rate within an individual as among individuals.

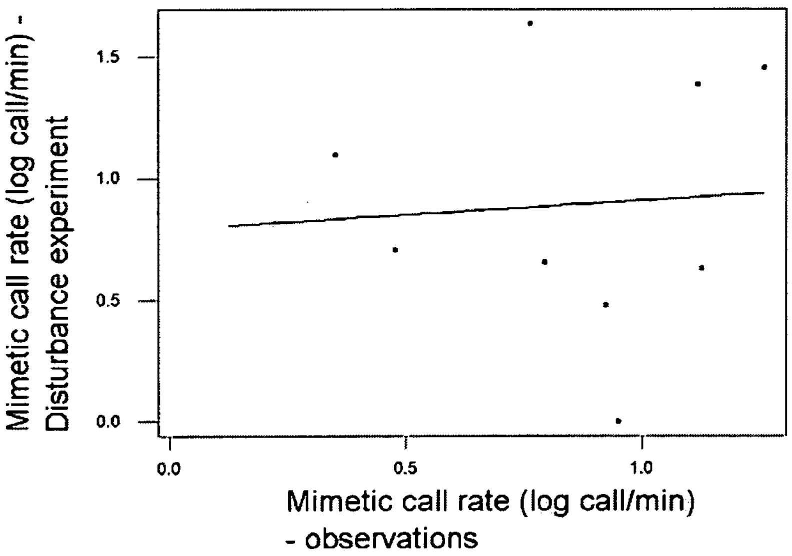


Fig 5.12: Non-significant relationship between individual mimetic call rate in the disturbance experiment versus mimetic call rate during observations

Individuals also varied in the size and composition of their repertoires, fig 5.13 summarises these findings. As detailed in chapter 3, this bar chart also highlights the tendency to preferentially mimic aggressive models. Observed repertoire sizes ranged from 2 to 14. The most common model was the magpie, mimicked by 16 individuals and the least common was the red winged parrot, mimicked by just two individuals.

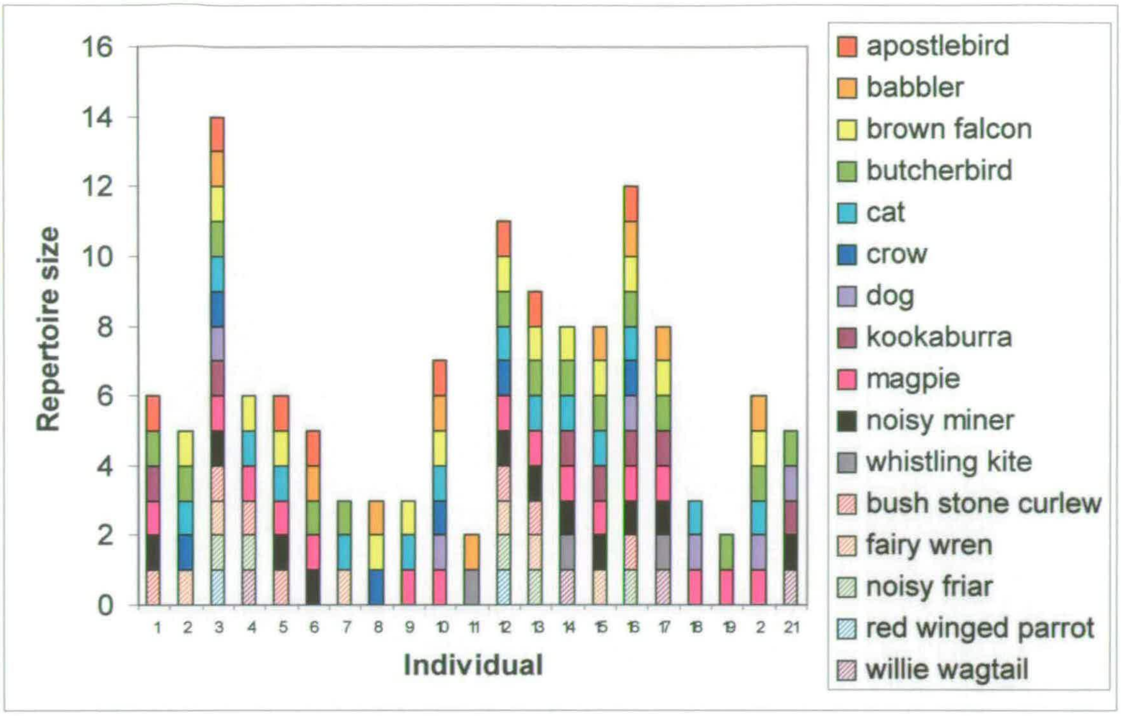


Fig 5.13: Size and composition of the mimetic repertoires of 21 ringed bower owners over both years. (Solid colour represents aggressive models (extreme assumption, see section 3.2) and striped colours represent non-aggressive models).

Status

There was no correlation between mimetic rate and status (GLM: individual: $F_{27,330}=3.18$, $p<0.001$, status (owner or auxiliary): $F_{1,27}=0.30$, $p=0.586$). The mimetic rate of unringed and ringed individuals of unknown status was also not significantly different (GLM: status (owner, auxiliary or unknown): $F_{2,31} = 0.16$, $p=0.852$).

A paired t-test comparing the observed repertoire sizes of auxiliaries to the owner of the same bower showed that the owners' repertoires were significantly larger (see 5.14, n=6, t=-3.40, p=0.019). This analysis could not be repeated using estimated repertoires as it was only possible to calculate these for three auxiliaries.

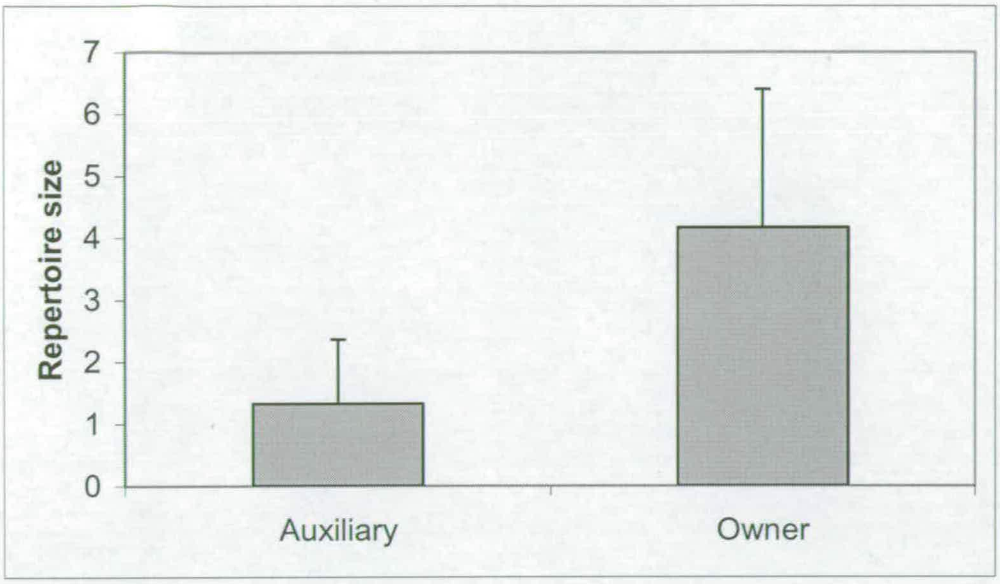
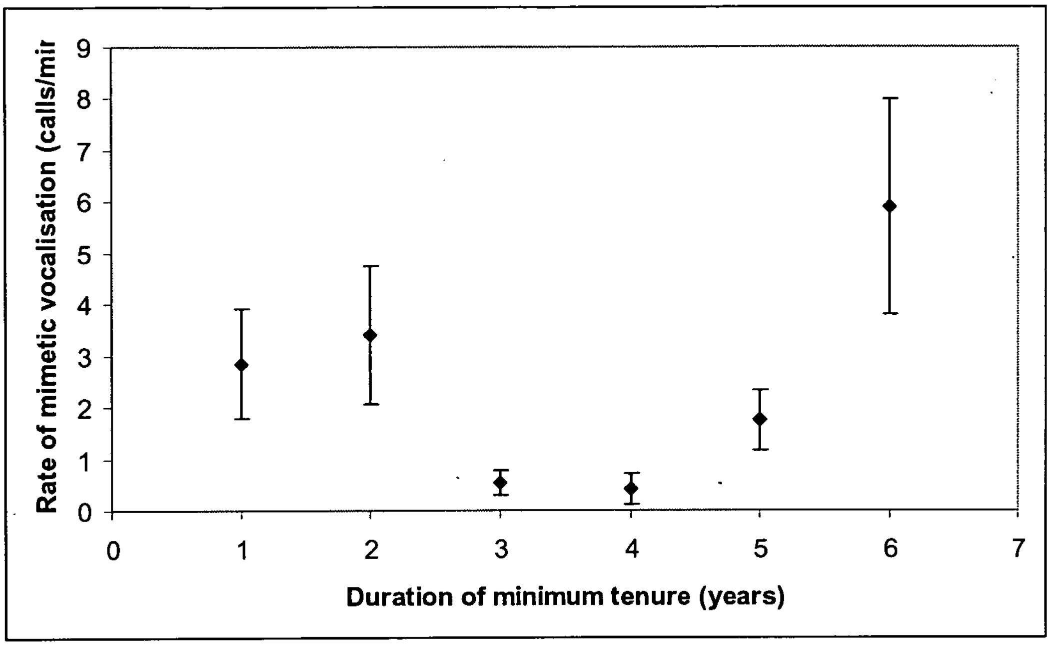


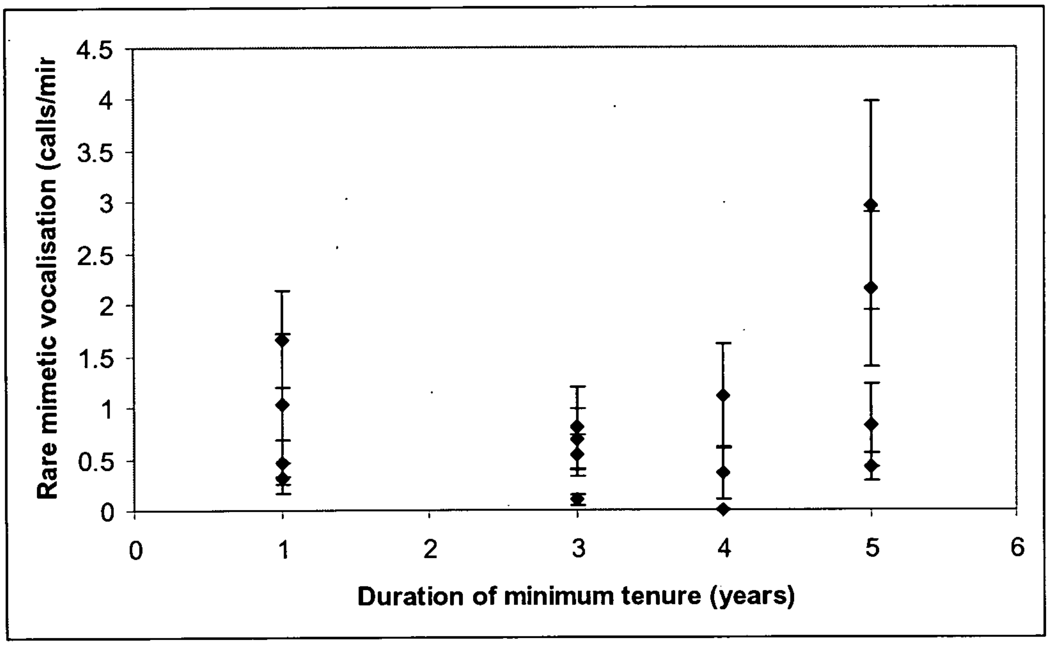
Fig 5.14: Difference in repertoire size in owners and auxiliaries at the same bower. Bars show mean repertoire size ± SD (n=6)

Duration of tenure

As with species-specific call rate, there was a highly significant effect of length of tenure as bower owner on mimicry rate (GLM: individual $F_{20,310}$=5.11, p<0.001, min tenure (co-variate) $F_{1,310}$=23.87, p<0.001, see fig 5.15 a, b and c). There was a tendency for mimetic rate to increase with length of tenure in individuals with a known tenure length (GLM: individual $F_{9,141}$=5.93, p<0.001, known tenure $F_{1,141}$=21.20,p<0.001, see fig 5.16). There was, however, no difference between individual average rate of mimicry in the two years (paired t test: t=-1.76, d.f.=12, p=0.106). The rate of mimicry varied significantly between experiments (see above), in particular the rate of mimicry was higher during the disturbance experiment. With this in mind the above analyses were repeated without the data from the disturbance experiment and all three results were qualitatively the same.


Rate of mimetic vocalisation (calls/mir
0
1
2
3
4
5
6
7
8
9
0
1
2
3
4
5
6
7
Duration of minimum tenure (years)

a)


Rare mimetic vocalisation (calls/mir
0
0.5
1
1.5
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2.5
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1
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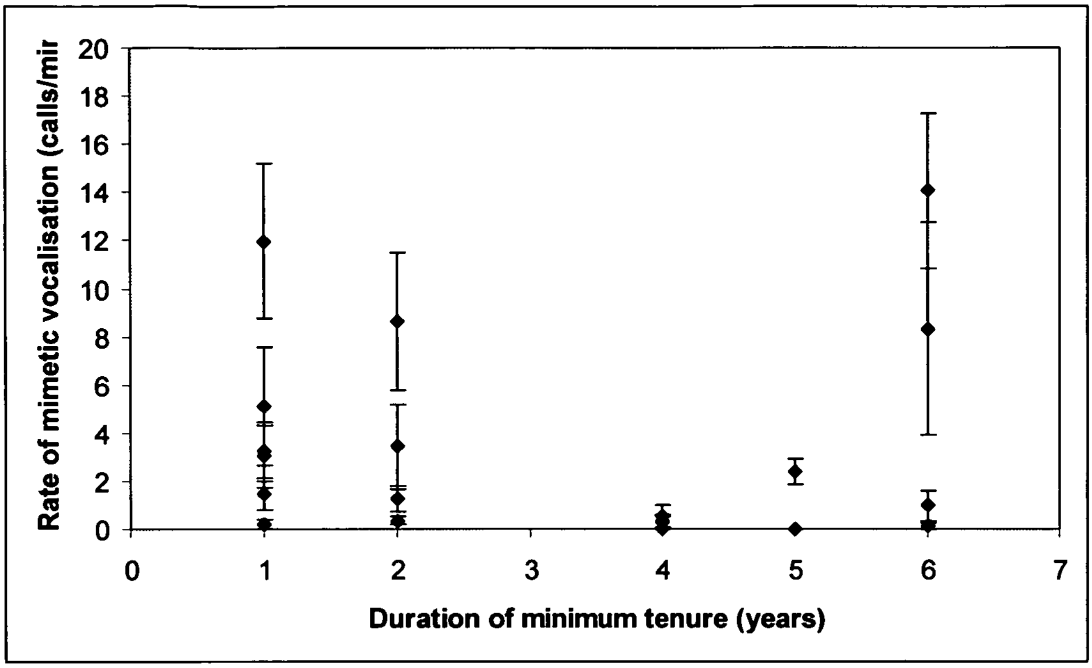
3
4
5
6
Duration of minimum tenure (years)

b)



c)

Fig 5.15: a-c) The relationship between the rate of mimetic vocalisation and minimum length of tenure a) for all bower owners (n=21) b) mean rate for all bower owners in 2001 (n=14) c) mean rate for all bower owners in 2003 (n=19). Points are means (± SE)

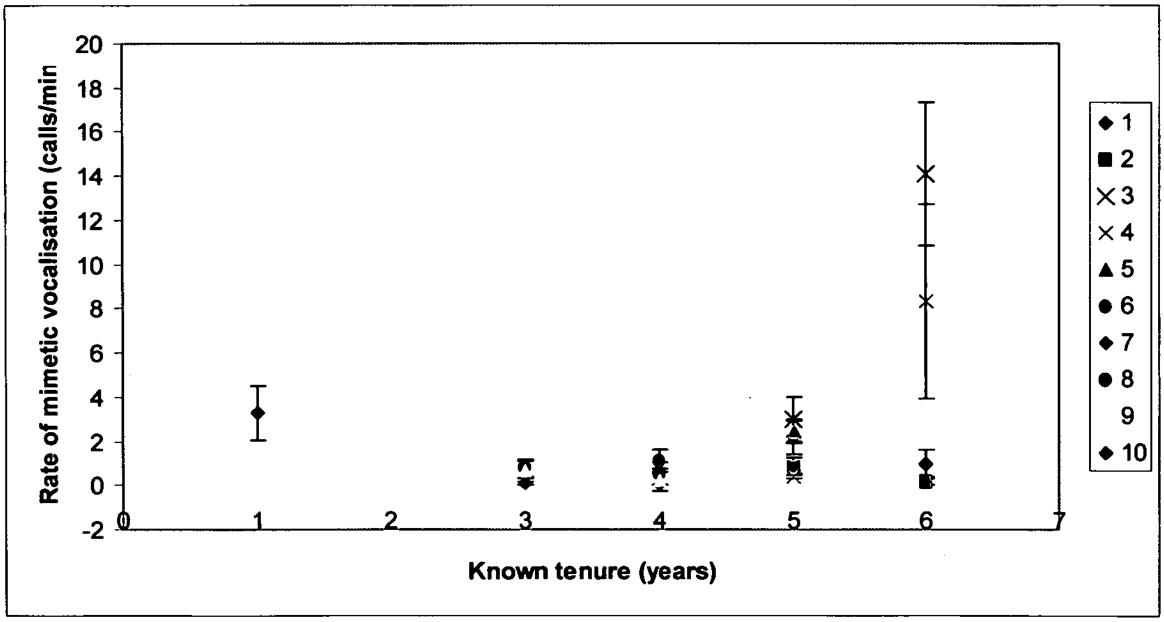


Fig 5.16: Individual rate of mimetic vocalisation (mean ± SE) for bower owners (n=10) against known bower tenure. Bower owners 5 and 6 were only observed in one year of the current study and 1 was a new bower owner in 2003.

There was a marginally non-significant relationship between mimetic repertoire size and length of bower tenure and a significant effect of individual (GLM individual (random) $F_{21,10}$=3.00, p=0.038, minimum tenure (covariate): $F_{1,10}$=3.86, p=0.078). Although there was a relationship between tenure length and mimetic repertoire size in the ten individuals of known tenure, there was no obvious pattern (GLM individual: $F_{9,4}$=41.72, p=0.001, known tenure $F_{1,4}$=40.00, p=0.003, see figs 5.16 and 5.17).

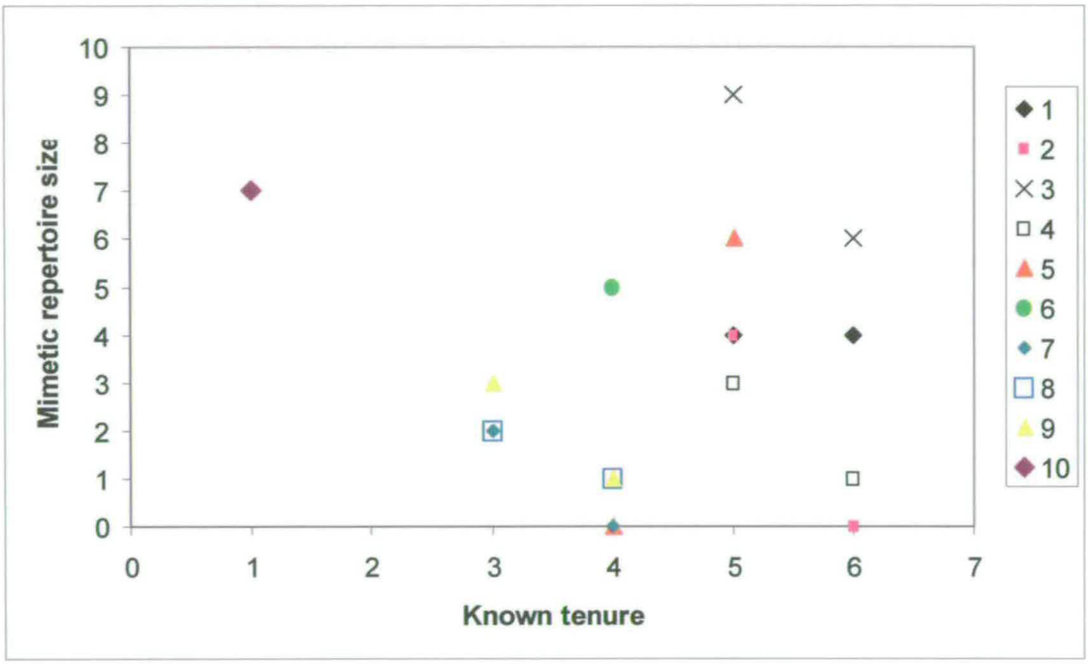


Fig 5.17: Repertoire sizes for individual bower owners (n=10) against the known duration of tenure

Repertoire size and composition over time

There were only 12 bower owners that were observed mimicking in both years. There was a significant difference between the observed individual repertoire sizes in 2002 and 2003 (paired t-test: t=2.38, d.f.=11, p=0.036, fig 5.18). There was also a significant difference between years in the estimated individual repertoire sizes (t=2.51, d.f. = 8, p = 0.036, NB the lower sample size is because estimates could not be made for birds with very small repertoires). In both cases the repertoire sizes were greater in 2002 than 2003. There was also variation in the composition of individual repertoires between the two years (fig 5.18).

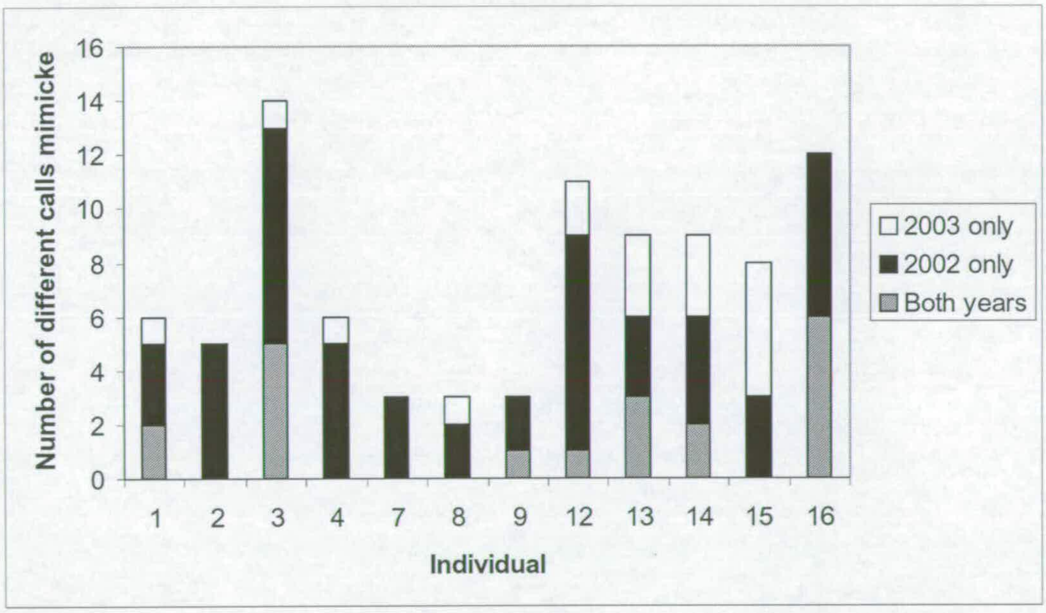


Fig 5.18: Change in composition of observed mimetic repertoire for ringed bower owners (n=12) in two years of study

Discussion

Individuals vary in the rate of their mimetic vocalisation and the low repeatability measure shows that intra-individual rate variation is similar to inter-individual variation. In particular, mimetic rate increased during simulated bower disturbances, in at least some individuals (see chapter 4). Although the comparison of mean mimetic rate during the disturbance to the mean observational rate, was marginally non-significant, the sample size was very small (just five individuals). It seems likely that there is a real effect that would be more apparent with a larger sample size. There was also a significant variation in rate among the different experimental procedures, largely due to the elevated mimetic rates during the disturbance experiment. These findings both suggest mimicry is used in specific circumstances (see chapter 3 and 4).

There is also considerable variation in the size and composition of individual repertoires. Overall, there are more aggressive birds mimicked than non-aggressive and within individuals non-aggressive models make up no more than half of the mimetic repertoire. This supports the results in chapter 3 that aggressive species are preferentially mimicked, potentially as a type of Batesian mimicry.

Bower owners do not mimic at a different rate to auxiliaries or unringed birds, but they do have larger repertoire sizes. By comparing owners and auxiliaries at the same bower, I attempted to reduce the confounding factor of duration of recordings. However, it is still the case that owners spend more time at the bower than their auxiliaries do, and so are recorded more often (see 5.2). Auxiliaries may be younger birds who will inherit bowers in the future (Madden et al., In prep) and have not obtained large mimetic repertoire yet, or they may be inferior birds unable to maintain their own bower or mimic large numbers of models.

Both repertoire size and mimetic rate correlated with duration of tenure, although the relationship was not obvious. There was an overall tendency for mimetic rate and repertoire size to be higher in individuals with the longest tenure; there are several possible explanations for this. Firstly, birds with a larger mimetic repertoire and higher rate might survive longer. This would support the hypothesis of mimicry acting as an effective threat avoidance tactic. Alternatively, it could suggest that repertoire size increases with age, with birds possibly learning new mimetic calls throughout their lifetime and hence also mimicking more often. Finally, it might be that the most successful birds, i.e. those that can hold a bower longest, also have the largest mimetic repertoires and highest rates of mimicry. Three of the five birds observed to mimic during the simulated disturbance (see chapter 4) were owners for five or six years. Although, obviously, this is too small a sample size to draw any strong conclusions from, it might also suggest that older males are more likely to use mimicry in response to a threat.

Individuals' repertoire composition did appear to change from one year to the next. This may be due to failure to capture all mimicry types from each individual in both years. It cannot be deduced from these data that repertoire size increases by incorporating new models into the repertoire, if anything, there was a decrease in repertoire size in the second year. Differences in repertoire composition between the two years could either be due to the use of a different selection from a repertoire learnt previously, possibly during a sensitive period, or because birds have learned new calls from the environment in the intervening year.

Older satin bowerbirds (*Ptilonorhnychidae violaceus*) have mimetic calls that are of higher structural integrity (quality) and of longer duration than younger bower owners (Loffredo & Borgia, 1986). However, there is no data on change in these song characteristics over an individual's life-time. Loffredo and Borgia also did not consider repertoire size, as their population appears to incorporate only two models into their courtship song. Over the course of that two-year study the duration and quality of the mimetic song was correlated to mating success in one year but not in the other. In mockingbirds (*Mimus polyglottos*) mimetic repertoire size is positively correlated with territory size, which influences mating date and presumably male fitness (Howard, 1973). There is, therefore, some slight, but not compelling, evidence for a link between characteristics of mimetic vocalisation and mating success. It would be informative to study individuals of these species, as well as spotted bowerbirds, over a lifetime. Tracking their mating success and changes in mimetic repertoire size and mimetic quality of individuals over a number of years. In spotted bowerbirds this would help to elucidate the relationship between tenure length and repertoire size and also how the repertoire composition changes over time.

5.4 Origins of individual mimetic repertoire

The mechanism for learning mimicry is largely unknown (Dobkin, 1979). It has most often been suggested that vocal mimicry is learnt from conspecifics (Hindmarsh, 1984; Eens at al. 1992), possibly from neighbouring males in a similar way to species-specific song learning in many birds (McGregor & Krebs, 1984). Alternatively, mimicry could be learnt from related individuals, although in bowerbirds this would not be from the father, as males play no part in rearing offspring (Catchpole & Slater, 1995). Mimicry might also be copied directly from heterospecific models (Dowsett-Lemaire, 1979).

In Chapter 3, I showed that spotted bowerbirds are not preferentially mimicking the most commonly heard birds on the national park. However, within the field site there are different types of habitat and, consequently, differences in local avifauna. In this section I look at whether the birds heard most commonly around a particular bower influenced the mimicry of the owner (or auxiliary) at that bower. If individuals do mimic the models most frequently heard at their bower this would support the learning mistakes hypothesis, with copying of common calls happening on a finer scale than the park in general. If there is no relationship this, along with the data from chapter 3, might mean that mimicry in the spotted bowerbird is unlikely to be explained by mistakes made during song learning and does not support the hypothesis that learning is directly from the models.

Closely related individuals could share more mimicry than more distantly related individuals because they have shared a common past or are genetically predisposed to mimic the same models. Male bowerbirds do not help to rear their offspring so there is no opportunity for young birds to learn from their fathers. Female bowerbirds have been observed to mimic whilst on the nest and whilst defending young chicks (Warham, 1962, Frith & Frith 2004). Siblings and half-siblings might therefore be exposed to the same mimicry early in life. It is conceivable that mimicry is transmitted from mothers to offspring, although this has not been documented (Frith & Frith, 2004). Alternatively, if females nest in the same area from year to year, related individuals may share similar acoustic environments during the first few weeks of life. I look for a correlation between similarity of mimetic repertoires and degree of relatedness (based on AFLP) using Mantel tests.

While it is difficult to determine how calls are learnt from studying adult birds with established repertoires, I look for similarities between individual repertoires and the local avifauna, and the repertoires of geographically close or related individuals. If these similarities exist it may suggest or eliminate some potential origins of mimetic repertoires. For example, if an individual bowerbird copied the calls heard most frequently at its bower, this might suggest that mimicry is arising due to mistakes in song learning and that they are directly copying the models. If geographically close individuals mimic more similar calls than more distant individuals, this might suggest that there is some sort of cultural learning with bowerbirds learning their mimicry from other bowerbirds (if copying from local, potentially similar, avifauna can be excluded). Finally, if related individuals share more mimicry than expected by chance this might suggest either that they are influenced by a genetic predisposition to mimic certain models or that they learn mimicry early in life, in a common environment. These hypotheses are not mutually exclusive. For example, individuals might pick up mimicry from neighbouring males and related individuals. Failure to find any link between individual repertoire and local avifauna, related or nearby individuals might suggest that the origin of the mimetic repertoire is from another source or that there is interplay between these sources which obscures a simple relationship.

Methods

Mimetic repertoire and bower avifauna

As described in section 3.2, during observations a census of all calls heard at the bower was taken for one minute in every five. The number of times each species was heard at each bower was recorded.

For each of the 21 ringed bower owners (and also three auxiliaries) the mimetic repertoire was taken as all the different types of mimicry identified in observations and experiments (see section 5.2).

To test whether more commonly heard calls were mimicked preferentially, the proportion of common calls mimicked was compared to the proportion of rare calls mimicked for each bird at each bower. At each bower, the species heard were divided either side of the median into "rare" and "common". Due to several birds sometimes being heard the same number of times as the median, there were two possible ways of defining rare and common:

1) "common" birds are heard more often than or equal to the median, "rare" birds less often
2) "common" birds are heard more often than the median, "rare" birds less often or equal to it

As the distinction is arbitrary, both categories were tested. It was not always possible to identify birds to species level by calls alone, hence they were clumped into related groups. For example, red-backed fairy wren and variegated fairy wren were grouped as “fairy wrens”.

For each individual bowerbird I recorded whether or not a particular model was mimicked. The proportion of common and rare birds (at this bower) mimicked was then calculated.

Geographic distribution and similarity of repertoire

The distance between each bower in 2002 and 2003 was calculated using the GPS positions (accurate to approximately 15m). This resulted in a matrix comparing each bower to every other bower that was studied in the same year (see appendix A.8). A similar matrix (with individual bower owners in the same order) was compiled comparing the proportion of mimetic calls shared. Individuals along the left hand side of the matrix were designated the focal individuals, the values along each row were the number of mimetic calls shared by this focal individual and the individual at the top of the column expressed as a proportion of the focal individual’s repertoire size (see table 5.6 and 5.7). This created an asymmetric matrix.

Individual	A	B	C
	apostlebird brown falcon bush stone curlew cat crow kookaburra magpie willie wagtail	babbler crow magpie noisy miner	apostlebird babbler brown falcon crow fairy wren noisy miner
Repertoire size	8	4	6

Table 5.6: example data for the comparison of repertoire composition amongst hypothetical individuals

Focal individual	**Compared to:**		
	A	**B**	**C**
A	na	(calls shared with **B**)/(repertoire size **A**) 1/8=0.125	(calls shared with **C**)/(repertoire size **A**) 3/8=0.375
B	(calls shared with **A**)/(repertoire size **B**) 1/4=0.25	na	(calls shared with **C**)/(repertoire size **B**) 3/4=0.75
C	(calls shared with **A**)/(repertoire size **C**) 3/6=0.5	(calls shared with **B**)/(repertoire size **C**) 3/6=0.5	na

Table 5.7: matrix showing proportion of calls shared by hypothetical individuals

I used a Mantel test to determine if pairwise distances between bowers are correlated to the proportion of shared mimetic calls (Mantel nonparametric calculator, Vers. 2.0, Liedloff 1999). Ten thousand random iterations were used for each test (one test for each year) and the input type was selected as full matrix without diagonals.

I also compared the mimetic repertoires of auxiliaries to the owners at the same bowers.

Relatedness and similarity of repertoire

Genetic analysis of 10 bowerbirds from the current study was carried out in collaboration with Dr J. R. Madden as part of a larger study, during which I assisted with DNA extractions and AFLP methodology (see Madden et al., 2004 b and c).

Relatedness was calculated based on amplified fragment length polymorphism (AFLP). In brief, DNA extractions from each bird were digested using DNA restriction enzymes (*Taq*I followed by *Eco*RI). Adapters, short pieces of DNA complementary to the cut ends left by the restriction enzymes, were ligated to the DNA fragments to generate template DNA. This was then bound to primers, which were complementary to the adapters except for an additional three bases at one end. Primers therefore selectively bound to fragments with the complementary sequences and these fragments are amplified using PCR. In this instance nine primer combinations were used, yielding 125 loci that could be scored. The PCR products were loaded and run on a polyacrylamide gel. The reaction products were visualised by autoradiography producing a series of bands for each individual. The AFLP markers are assumed to be unidominant, such that a band is either present or absent, with present being dominant to absent. The probabilities of different genotypes occurring were then calculated and used in Queller and Goodnight's (1989) formula to give a measure of relatedness (r). The larger the estimated value of r, the more related the individuals (see Madden et al. 2004 b for full protocol and also Mueller and Wolfenbarger, 1999; Questiau et al, 1999).

As described above, the proportion of mimetic calls shared between a pair of birds was calculated for a focal individual to produce an asymmetric matrix. I used a Mantel test to determine if relatedness between individuals is correlated to the proportion of shared mimetic calls (Mantel nonparametric calculator, Vers. 2.0, Liedloff 1999). As before, one thousand random iterations were used for each test and the input type was selected as full matrix without diagonals.

Results

Mimetic repertoire and bower avifauna

Birds commonly heard at an individual bower were not preferentially mimicked by bowerbirds at that bower. In fact, there was a tendency for rare birds to be mimicked more often. This was true for either definition of rare and common, although using the second definition the result was only marginally significant (Wilcoxon matched pairs: 1) W=53, n=24, p<0.001, 2) W=81, d.f. = 23, p = 0.05, see fig 5.19). Some models were mimicked but not heard at that bower at all during my observations.

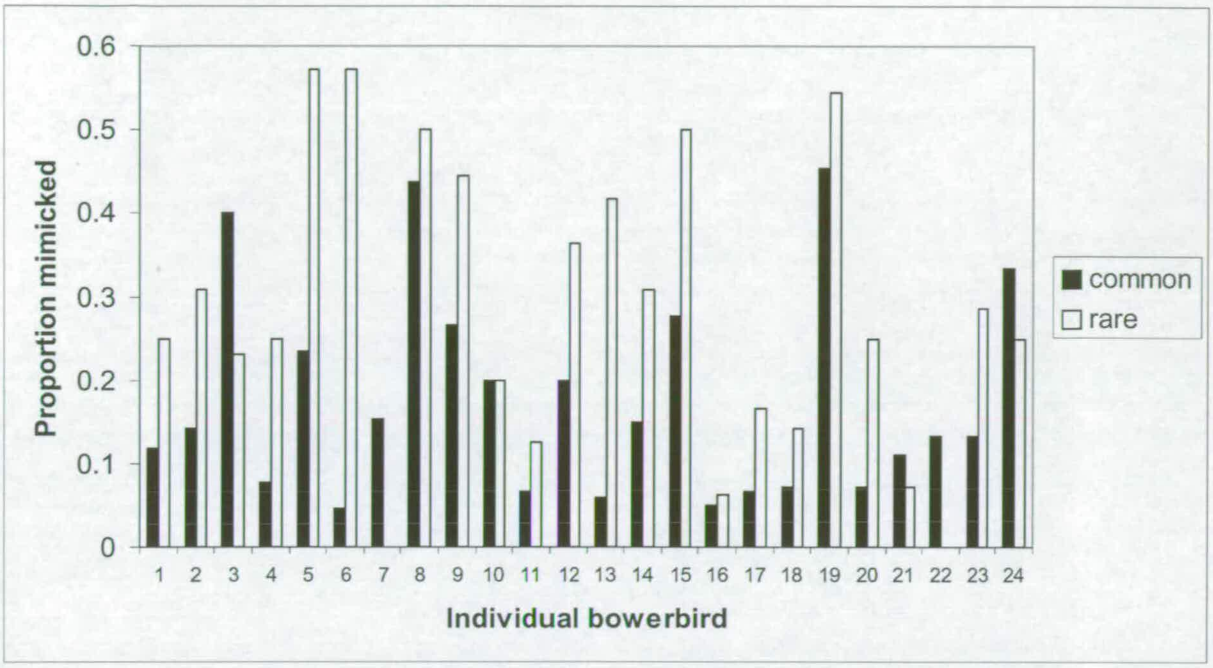


Fig 5.19: Bar chart showing the proportion of common and rare calls mimicked by individual bowerbirds (using definition 1 for common and rare).

Geographic distribution and similarity of repertoire

In 2002, there was a suggestion that geographically close bower owners share fewer mimetic calls than would be predicted (Mantel test: 14x14, r=0.1432, p=0.074). However, there was no tendency for a similar relationship using 2003 data (Mantel test: 19x19, r=0.0344, p=0.330).

There were only five ringed auxiliaries that were heard to mimic. Hence, there were insufficient data to carry out statistical tests comparing the composition of auxiliaries' repertoires to that of owners at the same bowers. However, half of the calls mimicked by the auxiliaries (5 out of 10) were also mimicked by the corresponding bower owner.

Relatedness and similarity of repertoire

I obtained relatedness measures for 7 ringed owners in 2002 and 8 in 2003. In neither year was there a relationship between relatedness and proportion of shared mimicry types (Mantel tests: 2002:7x7, r=-0.2575, p=0.109; 2003: 8x8, r=-0.1417, p=0.2150).

Discussion

Spotted bowerbirds are not preferentially mimicking the birds that are heard most often at their bower. This confirms the findings in Chapter 3 but on a more local scale. Spotted bowerbirds do not, then, seem to accidentally learn the most common calls in the environment. On the contrary, it appears that they mimic rare calls more often than would be expected. It is not obvious why bowerbirds would preferentially mimic rarely heard birds. It could be as a by-product of preferentially mimicking aggressive species, which might be less vocal, for instance some raptors. Alternatively it is plausible that the bowerbirds become habituated to commonly heard calls and rare ones are therefore more striking (Lorenz, 1964). If mimicry was involved in sexual displays, males could use rarely heard calls to prevent possible confusion amongst potential mates. There could even be selection for rare or novel calls that are difficult to learn if they were better indicators of male quality (ten Cate & Bateson, 1988; Gil & Gahr, 2002). There is no evidence from this data that bowerbirds are copying from the model directly, but the possibility cannot be excluded.

Other studies have previously looked for a link between local avifauna and mimetic repertoire composition. Hindmarsh (1984) found that European starlings mimicked more abundant species on the Fair Isle and cites this as evidence for the learning mistakes hypothesis. However, he did not look at how often these birds were heard. It has been suggested that many of the migrant birds are unlikely to have been vocalising whilst on the island (P.J.B. Slater pers comm.). Hamao and Eda-Fujiwara (2004) also suggest the learning mistake hypothesis explains mimicry in the black-browed reed warbler (*Acrocephalus bistrigiceps*). They claim that the warblers mimic common birds in their environment but they do not report the data to support this statement. Fergusson et al. (2002) found no correlation between the number of times a bird was heard and the number of times it was imitated by African robin chats (*Cossypha spp.*). None of these studies, however, looked at the immediate sound environment of an individual and I am not aware of any study that has done so.

There are several limitations in the interpretation of the data presented here. Firstly, if there is a sensitive period (and there is no evidence as to whether there is or not) during which mimicry is learnt, it is likely to be early in life before a male has established himself at a bower. Model species commonly heard at feeding grounds or at practice bowers may, therefore, make up a larger proportion of mimicry than those heard at adult bowers. However, having looked at both the global composition of avifauna on the park, and the more local avifauna at each of the bowers, it seems unlikely that the composition of birds at feeding sites would be greatly different from either of these. Secondly, my data are limited to the period between June and December. I have no data on the frequency with which birds were heard outside of this time. It is conceivable the bowerbirds preferentially mimic birds heard most frequently throughout the year, or at a specific time, for instance just after hatching (likely to be December to March in this population).

Thirdly, some birds are frequently heard but not necessarily making the call that the bowerbirds mimic. A prime example of this is the butcherbird (*Cracticus* spp.). Their melodious, flute-like song is one of the most frequently heard and easily identified at the field site. However, this is quite distinct from the sharp "eerik" call they make in distress, which is mimicked by the bowerbird. The butcherbird "eerik" call was so rare I was only able to obtain one good quality recording of it (although it was recorded on other occasions it was obscured by other calls). It would have been better to have measured the frequency with which each type of call from each type of bird was made but this would obviously be a huge undertaking.

Finally, the observations of the frequency with which species of birds were heard at bowers were limited by my ability to recognise them. It is probable that the likelihood of me recognising bird song was higher for common birds and perhaps also for birds mimicked by bowerbirds. This would have the effect of making common birds and mimicked birds appear more common, hence the results are likely to be conservative. Limitations in recognition are perhaps more significant at the other end of the scale such that rare birds may not have always been recognised with the result that they would seem even more rare. This leads me to doubt whether bowerbirds really are preferentially mimicking rarely heard birds.

There was no evidence that bower owners who were geographically close had more similar mimetic repertoires. In fact, in one year they appeared to be more dissimilar. It has been suggested local traditions arise in bower design due to neighbouring individuals visiting and copying each other's bowers (Diamond, 1986; Madden et al., 2004, see chapter 6) so these would also be prime candidates for transmission of mimicry. However, the data suggest mimetic calls are not being transmitted among neighbouring bower owners. Nearby bower owners being more dissimilar by chance is consistent with the hypothesis that mimicry is used in individual recognition (Harcus, 1977; Hausberger et al., 1991) and males might therefore actively avoid copying the same calls as their neighbours.

It seems possible that auxiliaries might copy the mimicry of the bower owner. However, auxiliaries do not exclusively mimic the same models as the owners at that bower. Complete mimetic repertoires for more auxiliaries would be useful for determining whether they share more mimicry with their corresponding bower owner than with randomly selected individuals.

It is not possible to rule out the transmission of mimicry between individual bowerbirds but it does not appear to occur between neighbouring bower owners or, as far as the data allow a conclusion to be drawn, between owners and auxiliaries at the same bower.

There is no evidence from the current data, that bowerbirds copy the same songs as more closely related individuals. This might suggest that there is no genetic predisposition to copy particular models nor is mimicry learnt in an environment shared by related individuals. However, the sample sizes are very small and these conclusions are therefore only tentative. It would be useful to extend the analyses to a larger number of individuals, ideally including known first-order relatives (i.e. parent-offspring or full sib pairs).

Spotted bowerbirds do not appear to be mimicking the most common avifauna, related or geographically close individuals. My observations can help to eliminate some potential origins of mimetic calls. Bower owners did not mimic the most commonly heard species, either at their bower or in the park in general (chapter 3). This suggests that mimicry is not due to learning mistakes (Hindmarsh, 1986) while not ruling out the possibility that the bowerbirds learn mimetic calls directly from the models. In fact, as individuals do not appear to share mimicry with neighbouring bower owners or related individuals, this is perhaps the most likely source. It is conceivable that they learn to mimic a selection of the available conspecific models, perhaps because physiological constraints limit the type of sounds they can produce (Kaplan, 1999). Alternatively, a variety of calls may be learnt and then through trial and error only those that are effective for the particular functions (e.g. deterring predators) are retained. This could explain the variation in repertoire composition between the two years of the study. It is also possible that bowerbirds are learning common calls at a time or location other than those studied here. Finally it is conceivable that mimicry is learnt from mothers before fledging.

The way birds learn vocal mimicry is poorly understood (Dobkin, 1979). This is despite the development of bird song being studied in greater depth than perhaps any other aspect of behaviour (Catchpole & Slater, 1995). Studies on captive parrots (Pepperberg, 1981) and European starlings (West & King, 1990) suggest that social interaction is necessary for the birds to pick up human speech. In the wild, it is thought that European starlings incorporate mimicry mainly from copying conspecifics, who occasionally make mistakes in learning and copy a heterospecific

(Eens et al., 1992; Hindmarsh 1986). Hence, several reports of sedentary starlings mimicking species that are found hundreds of miles away (Hausberger et al., 1991; P. J. B. Slater pers comm.). Some examples of vocal mimicry must be learnt directly from the heterospecifics, indeed even in species like starlings this must be the way the mimicry is initially incorporated into repertoire. It is not known whether there is a sensitive period for such learning, as there is for many species' own songs (e.g. Marler & Peters, 1987) or if new sounds are incorporated throughout the mimic's life, copied either from conspecifics or the heterospecific model.

There is considerable scope for future work. Firstly it would be useful to record the mimicry of females on the nest and to track individuals' mimetic repertoires through life. Ideally the vocal learning of captive bowerbirds would be studied, where the sound environment can be carefully controlled. It would also be informative to compare whether the structure of calls, rather than just the type, is more similar among related and neighbouring individuals. This could be done using principle component analysis (PCA, e.g. Hamao and Eda-Fujiwara 2004) and could help to show whether calls are culturally transmitted among bowerbirds.

5.5 General Discussion

In this chapter I have shown that there is considerable within and between-individual variation in species-specific rate in the spotted bowerbird. In particular auxiliaries have a higher rate of vocalisation than owners. There is also a tendency for the rate to be highest in long-term bower owners, although there was no evidence of change within an individual in the two years of study. Further work would include studying individuals for longer and recording the length of hiss as well as the rate as this has previously been shown to be important in mate choice (Borgia & Presgraves, 1998).

I used asymptotic and capture-recapture techniques to estimate complete mimetic repertoire sizes. I concluded that the capture-recapture technique was more useful because it took into account the heterogeneity of call occurrence and, unlike the asymptotic method, always produced biologically relevant estimates. It seems likely that for many individuals the observed mimetic repertoire is smaller than their complete mimetic repertoire size. I believe this to be the first time the capture-recapture technique has been applied to mimetic repertoires. There is a need for further discussion of the applicability of this technique to relatively small repertoire sizes, and rare and sporadic calls, like that of the spotted bowerbird mimicry.

There was variation in mimetic rate and repertoire size. Whilst there is no correlation between status and mimetic rate, owners have a larger repertoire size than auxiliaries. There was a tendency for mimetic rate and repertoire size to increase with bower tenure but individuals actually showed a decrease in repertoire size over the two years. Individual repertoire size (both observed and estimated) was positively correlated with the proportion of time during observations that the individual was present at the bower.

Differences in experiences may account for some of the observed differences in individual vocal traits. For instance, the occurrence of mimicry in response to a human disturbance (chapter 4) might only occur if the individual bowerbird has identified humans as a potential threat. It should be noted that all of the individuals studied in detail have had at least one potentially stressful and aversive experience with humans: that of being caught in a mist net, measured, ringed and in some cases undergone feather and blood extractions. Interestingly, mimicry was not observed during any of these interactions (pers obs, compared with Chu 2001). At first sight, this does not appear to support the hypothesis that mimicry is involved in threat avoidance, however if it is a type of Batesian mimicry this stage in the "predatory attack" is too late to fool the predator. A palatable mimic can no longer obtain the advantages of mimicking an aposematic species when it is in the jaws of a predator.

Finally, I have shown that bower owners do not copy the calls of heterospecifics that are heard most frequently around their bower. Nor do they show any tendency to share mimicry with geographically close or related individuals.

Chapter 6. Vocalisation, bower quality and individual differences

6.1 Introduction

The majority of studies on sexual selection in bowerbirds have focussed on the quality of the bower itself (e.g. Pruett-Jones & Pruett-Jones, 1983; Borgia, 1986; Humphries & Ruxton, 1999; Madden 2001b) Whilst the bower is obviously important in mating success, the display of a male bowerbird is an excellent example of a multi-component signal (Johnstone, 1997; Rowe & Skelhorn, 2004). There are visual cues, such as bower decorations (Borgia, 1985b) and male plumage (Doucet & Montgomerie, 2003), and also auditory cues (Borgia & Presgraves, 1998; Loffredo & Borgia, 1986) that correlate with mating success. Vocal traits, such as mimetic repertoire, might correlate with other predictors of mating success, possibly implying a role in sexual selection (Johnstone, 1995).

Vocalisation is an important component of sexual display in a variety of animals (Ryan, 1988; Simmons, 1995; ten Cate et al., 2002) and there is often a link between repertoire size and mating success (Hiebert et al., 1989; Adret-Hausberger et al., 1990; Mountjoy & Lemon, 1996). One hypothesis to explain the function of vocal mimicry in birds is that it increases repertoire size, and therefore attractiveness (Marshall, 1950; Dobkin, 1979). In bowerbirds, mimetic vocalisation is used in courtship displays in all genera, except *Chlamydera* and the monogamous catbirds (*Ailuroedus,* Frith & Frith, 1993; Frith & Frith, 2004). Only one study has looked directly at the relationship between vocal mimicry and mating success: Loffredo and Borgia (1986) found a positive correlation between the quality of vocal mimicry and the number of copulations in the satin bowerbird (*Ptilonorhynchus violaceus*).

Unlike for vocal traits, there have been many studies demonstrating that aspects of bower quality are positively correlated with mating success (Borgia & Gore, 1986;

Borgia & Mueller, 1992; Madden 2001b) and these measures have also been shown to correlate with each other (Borgia, 1985b; Borgia, 1995a; Patricelli et al., 2003). In particular, Borgia (1985b) found that the numbers of different bower decorations, that were good predictors of mating success, were highly correlated on individuals' bowers. There are far fewer studies that look at the correlation between different signals of multi-component displays (Johnstone, 1995; Johnstone, 1997; Patricelli et al., 2003; Rowe & Skelhorn, 2004). There are both theoretical suggestions (Johnstone, 1995) and some empirical evidence (Andersson, 1991; Nicoletto, 1993; Johnstone, 1997; Doucet & Montgomerie, 2003) that various measures of individual quality will correlate. In satin bowerbirds, the intensity of male ultraviolet plumage is positively correlated with bower quality and both traits are correlated with other features of male attractiveness (e.g. bower quality and ectoparasite load; plumage colouration and feather growth, Doucet & Montgomerie, 2003).

Although there is evidence that vocal mimicry is sexually selected in other species of bowerbird, it is not clear whether this is also the case for the spotted. My data from previous chapters suggests that sexual selection does not explain the occurrence of vocal mimicry in this species. Mimetic rate does not increase towards the breeding season or in the presence of conspecifics. However, I could not completely exclude the possibility that vocal mimicry may have a sexually selected function.

On the other hand, mating success does appear to be related to species-specific vocalisation in this species. Specifically, the ratio of long to short hisses is correlated with number of copulations observed at the bower (Borgia & Presgraves, 1998). My data on species-specific vocalisation is consistent with this. The rate of hisses increases in the presence of conspecifics and there is a tendency for the rate to increase towards the mating season.

Some indicators of male quality improve with age, thus potentially allowing females to choose to mate with older, more experienced males who have demonstrated good survival ability (good genes, Zahavi, 1975; Ryan, 1997). These indicators may be morphological traits, for example antler size in red deer *Cervus elaphus* (Kruuk et al., 2002), or behavioural like repertoire size or aspects of courtship display. In European starlings (*Sturnus vulgaris*) older males have larger repertoires, are more attractive to females and pair earlier (Eens et al., 1991; Mountjoy & Lemon, 1996). Similarly, the singing performance of cooperatively displaying long-tailed manakins (*Chiroxiphia linearis*) improves with age. The frequency of the song of displaying pairs of males becomes more closely matched and mating success increases with the duration of partnership and the age of the beta male (Trainer et al., 2002).

The quality of bower display may also increase with age. The bowers of younger birds are often poorly constructed and sparsely decorated (Pruett-Jones & Pruett-Jones, 1983; Diamond, 1986; Frith & Frith, 2004) and it has been suggested that bower construction has a large learnt component (Vellenga, 1970; Borgia and Collis, 1993; Maxwell 1999 as cited in Madden 2001b). The best evidence for an age-related improvement in bower quality comes from satin bowerbirds, where juvenile males that attain adult plumage prematurely after testosterone implants built poorer quality bowers than more experienced adult males (Collis & Borgia, 1993). I am not aware of any study that follows the change of bower quality in unmanipulated males for more than two years.

The year may have a confounding effect on the changes in bower quality during a male's tenure. In particular, availability of favoured natural decorations, like *Solanum* berries, might vary among years due to variation in rainfall or other environmental factors. Spotted bowerbirds do not preferentially chose rare, and therefore costly, objects as bower decorations (Madden & Balmford, 2004a). However, the relationship between fluctuations in availability of natural decorations and their use on bowers has not been explored.

I begin this chapter by considering whether there is a relationship between vocal traits (such as hiss rate and mimetic repertoire size), and bower characteristics (see below) that are known to correlate with mating success. In the absence of direct observations of mating success, such relationships might suggest whether these vocal traits are used in a sexual context. As a comparison I also look for correlations among the measurements of bower quality. I then look at individual variation in bower quality (Borgia, 1986; Diamond, 1988; Madden & Balmford, 2004b) and whether this can be explained by improvement with male age (cf. Collis & Borgia, 1992; Collis & Borgia, 1993). I look at whether four measures of bower traits that were correlated with mating success and one that was not, change during the course of bower tenure. Finally, I assess whether environmental availability of a preferred decoration can explain its occurrence on bowers (Madden & Balmford, 2004a), by looking for relationships between the occurrence of *Solanum* berries, plants and flowers and the number of *Solanum* berries at bowers.

Throughout the chapter I look at four bower characteristics that are positively correlated with mating success in spotted bowerbirds: 1) total number of bower decorations (Borgia, 1995a), and satin bowerbirds (Borgia, 1985b; Hunter & Dwyer, 1997); 2) number of *Solanum* berries at the bower (Madden, 2001b; Madden, 2002; Madden, 2003); 3) measures of bower symmetry (Borgia & Mueller, 1992); 4) overall bower quality (Borgia, 1995a; Madden, 2001b) and regent bowerbirds, *Sericulus chrysocephalus* (Lenz, 1994). In addition, the number of *Eremophila* berries was recorded at the bowers. Although these berries are a common bower decoration, a similar size and colour to *Solanum* berries, and decay at a similar rate (Madden & Balmford, 2004b), they do not appear to be correlated with mating success (Madden, 2001b) and, therefore, form a useful comparison to the use of *Solanum* berries as decorations.

6.2 Methods

Between 1998 and 2003, 30 active bower sites were located on (and nearby) Taunton National Park. During this time, measurements were taken at 88 active bowers belonging to 41 ringed males. Data prior to 2002 are used with kind permission of Dr J. R. Madden. Bowers were visited between late September and early October, the period just prior to mating events (Madden 2001b), between 1998 and 2003 (with the exception of 2001 when no data were collected).

Number and type of bower decorations

All objects found on the bowers were counted, when more than 100 of a type of decoration (e.g. snail shells) were found the number was estimated to the nearest ten. As part of these counts, the number of *Solanum* and *Eremophila* berries at each bower was recorded.

Number of *Solanum* and *Eremophila* berries

In addition to the counts described above, between 10th June and 15th October 2002 and 21st June and 26th November 2003, each bower site was frequently visited and the number of *Solanum* and *Eremophila* berries present were recorded. In 2002, 15 bowers were visited on average every 7.1 days and in 2003, 20 bowers were monitored every 9.1 days. To standardise the data a single number represented the number of berries at each bower for a ten-day period, where more than one measurement was available a mean was taken.

Bower symmetry

The total height of the two walls was measured at five equidistant points along the length of the avenue. These five measurements were then averaged and the difference between the two walls was taken to give a measurement of symmetry. The internal length of each wall of the bower was measured at 10cm above the avenue floor. Again, the difference between left and right wall gives an indication of bower symmetry (Borgia, 1995b; Madden, 2001b).

Bower quality

Bower quality was judged on a scale of 0 to 4, where a score of "0" represented a complete lack of avenue wall and a score of "4" was awarded where the grass and stick component of the avenue walls was present and complete (see Madden 2001b).

Vocalisation traits

The repertoire size observed for each bower owner each year was recorded and an estimated repertoire size was calculated using capture-recapture techniques (see 5.2). The mean rate of species-specific and mimetic vocalisation was calculated from observations (see 2.13). Vocalisation data were only available for 2002 and 2003, so only the 21 owners during this period were included in the analyses of bower quality and vocal traits.

Bower quality and tenure

The change in bower quality with duration of tenure was studied in the 21 ringed bower owners that were owners for two or more years, except in a few cases where data for one male were missing. Analyses were also conducted on a subset of eight males for whom the duration of bower tenure was accurately known (see 2.9).

Solanum transects

Between 21st August and 24th November 2003 transects were carried out along an 8 km stretch of the main road running through Taunton National Park. The stretch was chosen because it provided disturbed earth, ideal for the growth of *Solanum* plants and also passed by close to several bower sites (3 bowers <200m, 5 < 1km). Random numbers were used to decide the starting point of each 20m transect, 20 of which were carried out per day. A tape measure was laid at the edge of the road and the number of individual plants within 1m either side of this line were counted. Any plant falling along the outer side of this line was included if over half of its area came within the designated area. The number of fully opened flowers and fully formed berries were also counted for each individual plant. The transects took place every three days, however in order to be consistent with the data collected at the bowers the results were collated to give average scores per 10 day period.

Statistical analysis

There were insufficient data to test interactions between year, tenure and individual, these were therefore assumed to be zero. The full model could not be tested on the eight individuals of known tenure due to lack of data, I therefore just tested the most relevant factors: individual (random factor) and duration of tenure (co-variate).

6.3 Results

Bower quality and vocalisation

Unsurprisingly, the three measures of *Solanum* berries at bowers were highly correlated (see table 6.1). There were also positive correlations between the number of *Solanum* berries and the total number of decorations at the bower, and between quality and total number of decorations. The difference between the height of the walls was negatively correlated with the total number of decorations; hence bowers with more symmetrical avenue walls had more decorations.

Measure of bower quality 1	Measure of bower quality 2	Pearson	p value
Total no. decorations	***Solanum* berries:** max. no at bower	**0.414**	**0.017**
***Solanum* berries:**			
average no.		**0.923**	**<0.001**
no. in Sept/Oct		**0.582**	**0.002**
Symmetry:			
difference in height		0.024	0.844
difference in length		0.095	0.599
Quality		-0.027	0.979
Total no. decorations	**Symmetry:** difference in height	**-0.44**	**0.01**
Symmetry:			
difference in length		0.057	0.755
Quality		-0.201	0.263
Total no. decorations	**Symmetry:** difference in length	-0.043	0.814
Quality		-0.208	0.246
Total no. decorations	**Quality**	**0.401**	**0.021**

Table 6.1 Summary of correlations between different measures of bower quality. Significant results shown in bold. (n = 21)

None of the measures of bower quality were significantly correlated with the measures of vocalisation (Pearson correlation, see table 6.2). There were marginally non-significant, positive correlations between the difference in wall height and the rate of species-specific hiss and between bower quality and estimated repertoire size (i.e. the owners of more symmetrical and high quality bowers tended to have lower rates of species-specific vocalisation and larger repertoire sizes). There was also a marginally non-significant negative correlation between difference in wall length and estimated repertoire size (the more symmetrical the bower, the larger the repertoire size). However, with multiple correlations such as these care should be taken against spurious results, obviously no results would be significant after the application of Bonferroni correction.

Measure of bower quality	**Measure of vocalisation**	**Pearson**	**p value**
Total no. decorations	**Observed repertoire size**	-0.079	0.66
***Solanum* berries:**			
max. no at bower		-0.064	0.724
average no.		-0.042	0.815
no. in Sept/Oct		0.203	0.331
Symmetry:			
difference in height		-0.194	0.28
difference in length		0.122	0.498
Quality		-0.171	0.342
Total no. decorations	**Estimated repertoire size**	0.255	0.199
***Solanum* berries:**			
max. no at bower		-0.156	0.436
average no.		-0.178	0.375
no. in Sept/Oct		-0.084	0.718
Symmetry:			
difference in height		-0.311	0.115
difference in length		**-0.378**	**0.052**
Quality		**0.346**	**0.077**
Total no. decorations	**Rate of species-specific vocalisation**	-0.179	0.32
***Solanum* berries:**			
max. no at bower		-0.185	0.303
average no.		-0.189	0.293
no. in Sept/Oct		-0.173	0.407
Symmetry:			
difference in height		**0.324**	**0.066**
difference in length		0.054	0.764
Quality		0.068	0.709
Total no. decorations	**Rate of mimetic vocalisation**	0.006	0.974
***Solanum* berries:**			
max. no at bower		0.151	0.41
average no.		0.052	0.777
no. in Sept/Oct		0.226	0.289
Symmetry:			
difference in height		0.062	0.738
difference in length		-0.177	0.332
Quality		0.033	0.857

Table 6.2 Summary of correlations between measures of bower quality and vocal traits. Marginally non-significant results shown in bold. (n =21)

Bower tenure and quality

Total number of decorations

Both the individual bower owner (GLM: $F_{20,39}$= 2.71, p=0.001) and the year ($F_{4,39}$ = 5.82, p=0.001) had a significant effect on the total number of bower decorations. The effect of length of tenure was non-significant ($F_{1,39}$ = 2.71, p = 0.107). Among the individuals of known tenure there was a significant effect of individual and (marginally) tenure (individual: $F_{7,21}$ = 2.5, p = 0.036; tenure: $F_{1,21}$ = 5.0, p = 0.049). The number of decorations declined with increasing duration of tenure (fig 6.1)

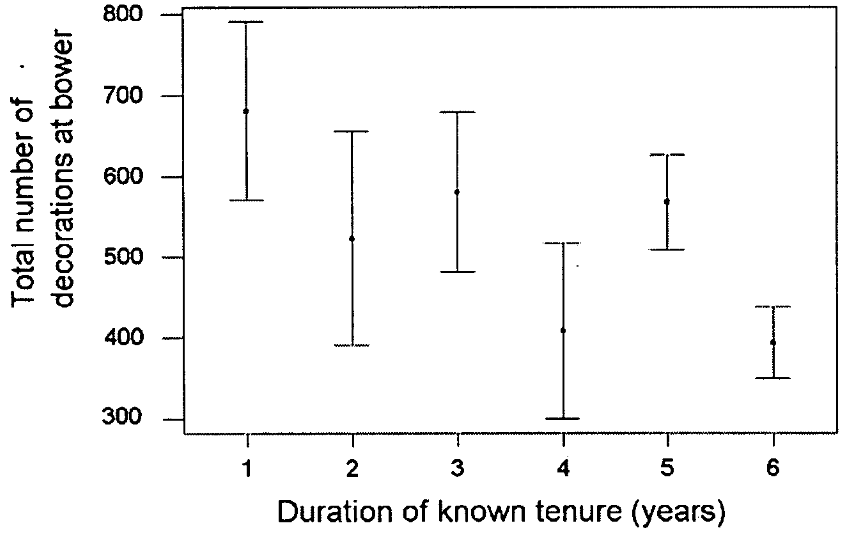


Fig 6.1: The total number of decorations displayed at the bower over duration of known tenure (Mean ± SE, n = 8)

Number of *Solanum* berries

The number of *Solanum* berries found at each bower was affected by neither the length of tenure ($F_{1,30}$=1.13, p=0.296) nor the individual bower owner ($F_{19,30}$=1.23, p=0.297). However, there was a significant effect of year with nearly seven times more berries being displayed in 1998, 2002 and 2003 compared to the other two years ($F_{4,30}$=5.89, p=0.001, see fig 6.2). There was no individual variation or an effect of tenure duration on the number of *Solanum* berries among the individuals of known tenure (individual: $F_{7,18}$ = 1.91, p = 0.127; tenure: $F_{1,18}$ = 1.83, p = 0.193).

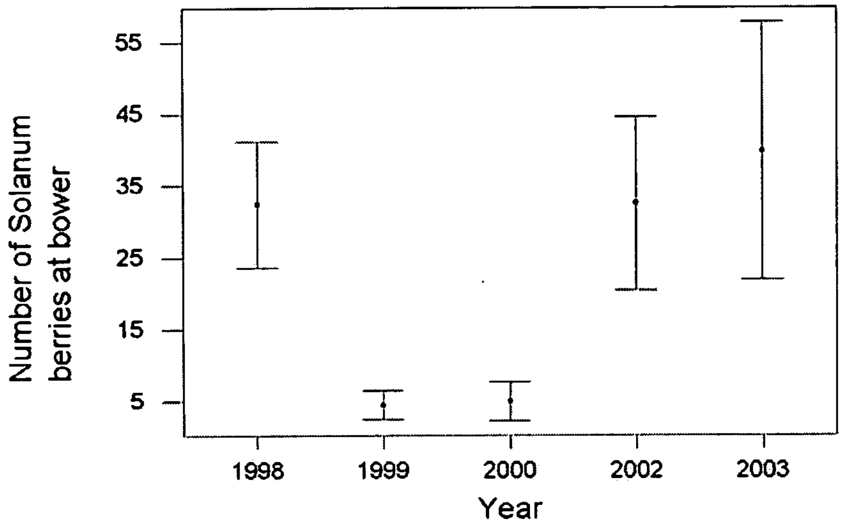


Fig 6.2: Number of *Solanum* berries displayed at the bower (in late September/early October) over the five years of study (mean ± SE)

Number of *Eremophila* berries

There was an effect of both year and individual on the number of *Eremophila* berries displayed at the bower (year: $F_{4,39}$ = 8.08, p<0.001 see fig 6.3; individual: $F_{20,39}$ = 4.44, p <0.001). The duration of tenure had no effect ($F_{1,39}$ = 0.71, p = 0.403). There was a significant effect of individual with known tenure, but still no effect of the duration of tenure (individual: $F_{7,21}$ = 3.60, p = 0.011; tenure: $F_{1,21}$ = 0.03, p = 0.876).

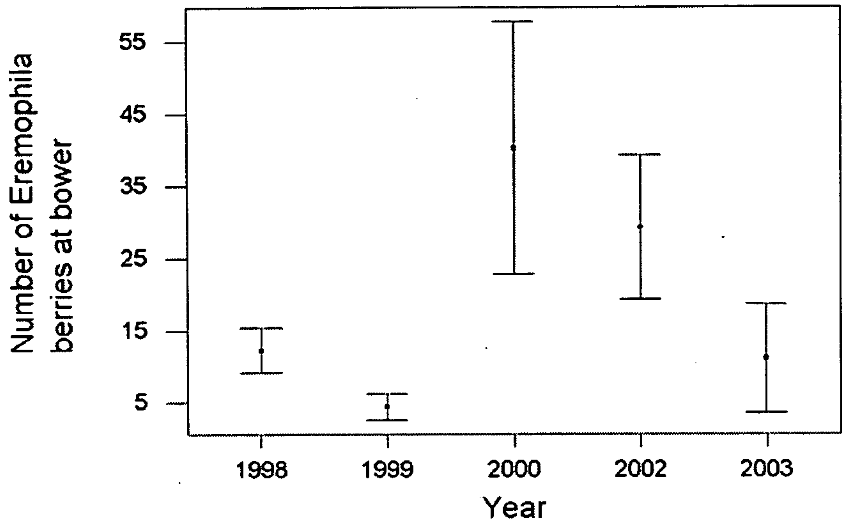


Fig 6.3: Number of *Eremophila* berries displayed at the bower (late September/early October) over the five years of study (mean ± SE)

Quality

There was a significant effect of individual on the quality of the bower ($F_{20,40}$ = 1.96, p= 0.035). Neither year and nor duration of tenure had an effect on bower quality, and tenure was dropped in the minimal model (year: $F_{4,20}$ = 1.27, p=0.297). There was no significant effect of tenure on the quality of bowers where the duration of tenure was known (tenure: $F_{1,21}$ = 0.63, p= 0.436).

Symmetry

Individual, duration of tenure and year had no effect on the difference in the height of avenue walls, even in the minimal model (individual: $F_{20,37}$ = 0.57, p=0.912; tenure: $F_{1,37}$ = 0.34, p = 0.564; year: $F_{4,37}$ = 1.56, p = 0.206). Similar results were found for the difference in wall length (individual: $F_{20,37}$ = 0.92 p = 0.571; year: $F_{4,37}$ = 1.37, p = 0.265; tenure: $F_{1,37}$ = 1.79, p = 0.188). There were also no significant effects on difference in height or length of walls among the bower owners of known tenure duration (height: individual: $F_{7,19} = 0.77$, $p = 0.619$; tenure: $F_{1,19} = 0.10$, $p=0.753$ and length: individual: $F_{7,19} = 0.85$, $p = 0.565$; tenure: $F_{1,19} = 0.56$, $p = 0.462$).

Environmental availability of a preferred decoration

There was no correlation between the average number of *Solanum* berries at the bowers and the average number of berries or flowers found in the transect for the same ten day period (Pearson correlation: r = 0.299, d.f. = 8, p = 0.401; r= -0.299, d.f. = 8, p = 0.403). There was a significant negative correlation between average number of plants in the transect and the number of berries at the bower (r = - 0.834, d.f. =8, p = 0.003, see fig 6.4). I also compared the number of berries at the bower with the transect measurements for the preceding ten day periods in case there was a lag between berries forming on the plant and being brought to the bower. The only significant correlation was a negative one between the average number of berries at the bower and the total number of plants in the transect in the previous 10-day period (r = -0.855, d.f. = 8, p = 0.002).

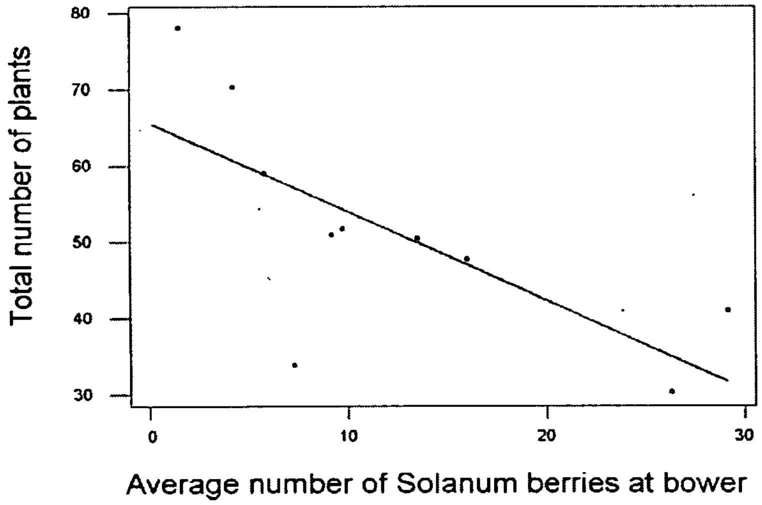


Fig 6.4: Relationship between the total number of *Solanum* plants in the transect and the average (across 20 bowers) number of *Solanum* berries at bowers

6.4 Discussion

Five of the twelve combinations of bower traits were significantly correlated. There were relationships between the total number of decorations and measures of symmetry (difference in height), quality and the maximum number of *Solanum* berries recorded at the bower. These correlations were in the expected directions, such that high quality bowers had more decorations and were more symmetrical. My results are consistent with previous high correlations among decoration variables and measures of bower quality that were also correlated with mating success (Borgia, 1985b; Borgia, 1995a). The correlation between different measures of bower quality is also consistent with them being good indicators of male quality (Borgia, 1985a), potentially used by females in mate choice (Coleman et al., 2004).

In contrast, there was little evidence from my data that bower and vocalisation traits were correlated. However, there were marginally non-significant correlations between the estimated mimetic repertoire size and bower symmetry (wall length) and bower quality. This was in the same direction as expected if mimetic repertoire size is an indicator of male quality (Zahavi, 1975). Superior males tend to have larger mimetic repertoires and build higher quality, symmetrical bowers. There was also a marginally non-significant negative correlation between bower symmetry (wall height) and rate of species-specific hiss. This might also be consistent with species-specific vocalisation being involved in sexual selection. The ratio of long to short hisses is correlated with mating success (Borgia & Presgraves, 1998). It has not been shown, but seems reasonable, that longer hisses would mean a lower rate of species-specific vocalisation. Hence, better quality males with a low rate of species-specific vocalisation make more symmetrical bowers. However, these results cannot be given too much weight as they were both marginally non-significant and the result of multiple correlations, which are likely to give Type I errors (Sokal & Rohlf, 1969). There were no significant correlations between the number of *Solanum* berries (the best predictor of mating success in 1998 and 1999, Madden, 2001b) and any of the vocal traits. These results provide no strong evidence for these vocal characteristics being involved in sexual selection.

Although my results suggested that the vocal traits examined here were not involved in sexual selection, there are alternative explanations for the lack of correlation between vocal traits and measures of bower quality. There is no consensus from theory as to whether different aspects of a multi-component signal should be positively correlated (Moller & Pomiankowski, 1993; Johnstone, 1995). Evidence from empirical studies is similarly contradictory. Doucet et al. (2003) found a positive correlation between two predictors of mating success in satin bowerbirds, male ultraviolet plumage and bower quality. However, Kraak et al. (1999) found no correlation among male sexual display traits in sticklebacks (*Gasterosteus aculeatus*). They suggest this is due to different traits revealing different aspects of male quality (the "multiple message" hypothesis; Johnstone, 1995) or being used in different contexts (i.e. inter- versus intra-sexual interactions, the "multiple context" hypothesis; Kraak et al., 1999). There is evidence from satin bowerbirds that females attend to different signal components depending on the stage of courtship (Coleman et al., 2004). In the current study, it is conceivable that male spotted bowerbirds initially attract females with their varied repertoire, for instance, and in later stage of courtship with their symmetrical bower or collection of berries.

It is also plausible that, while the vocal traits I studied here are not involved in sexual selection, others are. In particular the quality of mimicry and the length of species-specific hiss (Loffredo & Borgia, 1986; Borgia & Presgraves, 1998) might be correlated with measures of bower quality and thus be a useful indicator of mating success. I had planned to look at quality of mimicry using cross-correlation techniques to compare mimicry to model species (Feekes, 1982; Clark et al., 1987; Hile et al., 2000). However, I found that I did not have enough high quality recordings of each individual's mimicry or the models calls to address this issue without being confounded by pseudoreplication (Hurlbert, 1984; McGregor, 2000). It is an obvious area for future study not only on spotted bowerbirds, but satin bowerbirds and any other species where mimicry may be sexually selected for quality and/or accuracy to the original model (Loffredo & Borgia, 1986).

Stronger conclusions could have been drawn about the use of vocal mimicry and other vocal traits in sexual selection, if I had collected data on mating success and vocalisation traits in the same individuals. I was unable to measure mating success directly as I did not observe any copulations (except one presumed forced copulation). Previous studies (e.g. Borgia, 1985; Madden 2001b) have recorded copulations at the bower, using video cameras linked to motion sensors, but this was beyond the remit of the current study. The lack of ringed females – I did not see any – also meant that possible indicators of female choice, such as length of bower visitation (Lenz 1994), could not be measured either. Looking at the relationship between bower quality and vocal traits has limited value as the measures of bower quality that predict mating success in one year are not necessarily the best predictors in subsequent years (Diamond, 1988; Freeberg, 2000). However, some bower traits, that have been shown to correlate with mating success, did correlate with each other whilst there were no correlations between bower and vocalisation traits. Data in chapter 3 show that mimicry does not increase towards the mating season or occur at higher rates in the presence of conspecifics. Combined with the data in this chapter, it seems unlikely that vocal mimicry plays a major role in sexual selection in the spotted bowerbird.

Individual variation occurred in several bower traits: total number of decorations, number of *Eremophila* berries and quality. The duration of tenure only appeared to have an effect on the total number of decorations. This was only a marginally significant effect and was only apparent when just the owners with known tenure were considered. The total number of bower decorations decreased the longer an individual had been an owner. This is the opposite to what might be expected given that total number of decorations correlated with mating success (Borgia, 1995a; Borgia, 1985b; Hunter & Dwyer, 1997) and non-perishable decorations might accumulate at traditional bower sites (Pruett-Jones & Pruett-Jones, 1983). Perhaps more experienced bower owners are more selective in their bower decorations, and only collect those that females display a preference for. However, this was not supported by an increase in number of *Solanum* berries (the best predictor of mating success in 1998 and 1999, Madden, 2001b) or a decrease in number of *Eremophila* berries (not correlated with mating success, Madden, 2001b) with increased tenure.

There was no evidence from my data that males are improving the quality of the bower throughout their lifetime as owners (cf. Collis & Borgia, 1992, 1993). There was even a suggestion that quality might decline with the total number of bower decorations decreasing with tenure (Borgia, 1995a). However, previous studies (Collis & Borgia, 1992, 1993) only looked at the difference between juvenile males brought into adult condition with testosterone implants and adult male bowers. Other studies (e.g. Vogelkop gardener bowerbird, *Amblyornis inornatus*, Diamond 1988; satin bowerbird, Vellenga, 1970; Macgregor's bowerbird, *Amblyornis macgregoriae*, Pruett-Jones & Pruett-Jones, 1983) suggest that there is a marked difference in quality of bower structures between juvenile and adult bowers, but do not compare the same individuals' bowers over time, nor look at differences among owners of varying tenure duration. My data do not support the idea that the bowers of adult males change in a predictable manner, i.e. traits do not improve with duration of tenure. However, if female preferences for bower traits change over time, a bower display might change from year to year but not in a predictable or linear manner (Freeberg et al., 2002). Alternatively, it might be that annual improvements in bower quality are not necessary as it is the relative rather than absolute quality of bowers that are important in mate choice (e.g. Jang & Greenfield, 1998; see chapter 7).

The year had an effect on both the number of perishable decorations (*Eremophila* and *Solanum* berries) and also on the total number of decorations (although this could be influenced by large numbers of berries). These differences might reflect variation in decoration availability between years. However, the environmental availability of *Solanum* berries appeared to have no affect on the number displayed on bowers. This agreed with previous evidence that, although *Solanum* berries are good predictors of mating success, it is not because of their rarity and consequent cost (Madden, 2001b; Madden & Balmford, 2004a). The large effect of year on number of berries observed at bowers, may be caused by far greater fluctuations in availability between years than was observed during the hundred day period of this study. There was a negative correlation between the number of *Solanum* plants (but not berries) on the transect and *Solanum* berries at the bower. It seems most likely that this relationship arose due to both factors being correlated with time: the number of berries at bowers increases nearer to the breeding season, whilst the number of *Solanum* plants decrease, perhaps due to changing weather.

Measures of bower quality and decorations are good predictors of mating success (Borgia, 1985b; Madden, 2001b). I showed that several measures of bower quality were correlated with each other, however they did not correlate with vocal traits, such as mimetic repertoire size or species-specific rate. This suggests, along with my earlier results, that these traits do not play an important role in a sexual context. Variation in bower quality existed among males but neither the duration of bower ownership, nor fluctuations in environmental availability appeared to explain this variation. In the next chapter, I consider whether cultural influences can determine bower characteristics.

Chapter 7: Cultural influences on bower design

7.1 Introduction

The evolution and maintenance of elaborate male traits and female preferences for them has been the subject of considerable research (e.g. Andersson, 1994; Ryan, 1997). Early research focussed on the genetic basis for these traits and preferences, by way of runaway sexual selection (Fisher, 1930) or "good gene" models (Zahavi, 1975). The significance of non-genetic factors, especially learning, in determining traits and preference for them, has begun to be appreciated more recently (ten Cate & Vos, 1999; Freeberg, 2000). Males may learn aspects of their courtship display (e.g. Trainer et al., 2002) and females may learn the preference for certain traits, for instance, through mate choice copying (Ophir & Galef, 2004). Bower design is a possible example of culturally transmitted courtship behaviour (Freeberg, 2000).

Diamond (1986) showed that bower style in the Vogelkop gardener bowerbird (*Amblyornis inornatus*) varied between individuals and populations. For example, in one population coloured fruits were often used as decorations whilst in a second population just 8km away, such fruits were never used, despite being readily available. Diamond proposed two hypotheses to explain these observations. Firstly, males learn through trial-and error which bower decorations attract females. Localised female preference for particular traits could explain their geographic distribution, especially if potential mates modify the behaviour in males. This is observed in the brown-headed cowbird (*Molothrus ater*): a male is more likely to repeat certain song types if a female responds with a "wing-stroking" display (West & King, 1988) and female cowbirds show a preference for local dialect types, which appears to maintain distinct and stable local dialects (O'Loghlen & Rothstein, 2003). Localised female preferences for bower design have not been tested but male satin bowerbirds (*Ptilonorhynchus violaceus*) lessen the intensity of their display if females are startled (Patricelli et al., 2002). It is conceivable that feedback from females could influence bower design in a similar way and, if combined with localised female preferences, might result in local bower traditions. Diamond's second hypothesis was that males learn from each other, causing local traditions. In several species, juvenile males collaborate on practice bowers and attend fully formed adult bowers, during which time it is suggested they learn how to build their own bowers (Vellenga, 1970; Frith & Frith, 2004). In spotted bowerbirds some males act as an auxiliary to the bower owner assisting in bower maintenance; these might also learn bower design during this time (Madden et al., in prep).

Geographic and individual variation in bower decoration has also been shown in satin bowerbirds (Vellenga 1970), Macgregor's bowerbirds (*A. macgregoriae*; Pruett-Jones & Pruett-Jones, 1983) and, most recently, in spotted bowerbirds (Madden et al., 2004c). In the Taunton population of spotted bowerbirds, geographically close bowers were more likely to display the same types of decorations than bowers further away. Madden et al. (2004c) compared the occurrence or absence of 92 decoration types across all bowers and found more similar patterns in bowers that were close together. Such similarities cannot be explained by relatedness amongst neighbouring bower owners, variation in local availability in decorations, variations in local display conditions (i.e. light which could favour specific decorations) or stealing behaviour by neighbouring owners (Madden et al., 2004c). These very localised traditions could be maintained by cultural transmission amongst males or by response to local variability in female preferences, as suggested by Diamond.

A previous experiment (Madden and Fawcett, unpublished data) failed to find evidence for either trial-and-error individual learning or cultural transmission of preferences. Based on the fact that preferred decorations are displayed nearer the centre of the avenue whilst unpopular objects can be removed as far as 10m away (Madden, 2003b, see also Diamond, 1986), and thus, the distance an object is moved relative to the bower could be taken as a measure of preference, Madden and Fawcett presented two novel kinds of object (pink and orange glass chips) outside the bowers. Having determined, in an initial preference test, whether these were accepted (moved closer to the bower) or rejected (moved further away), half of the bowers were experimentally manipulated by attaching pink chips to just outside the avenue for 14 days. The pink chips were removed and the preference test, with both colours, was repeated at all bowers. If decoration preference were due to trial-and-error learning the preference for pink chips would have altered at the experimental bowers but not the control bowers. Alternatively, if decoration preference is culturally transmitted, the control owners might have altered their preference for pink, but not orange, counters as a result of observing them on neighbouring bowers. However, Madden and Fawcett found no differences in preference, either as a result of the forced exposure or between control and experimental groups, and concluded that their experiment did not provide evidence for trial-and-error learning or cultural transmission. However, one caveat to their conclusions was that the forced exposure was comparatively short, accounting for just 15% of the total display season (Madden and Fawcett, unpublished data). This may not have allowed enough time for an effect on male behaviour or for the control birds to visit their supplemented experimental neighbours. This is especially pertinent in spotted bowerbirds, as the wider spacing of their bowers compared to that of other bowerbirds (~ 1-2km, Borgia & Mueller, 1992; Miles & Madden, 2002 cf. satin bowerbirds: ~200-300m, Frith & Frith, 2004) means that male-male interactions are also less frequent. For example, bower destructions occur at a rate of 0.032 per day at spotted bowers compared to 0.20 per day at satin bowers (Borgia, 1995b).

The spatial distribution of similar bowers in spotted bowerbirds could, alternatively, be due to auxiliary males learning the bower design of the bower owner and then taking over that bower or one nearby. Not much is known about the acquisition of bower sites in the spotted bowerbird (Frith & Frith, 2004), partially because the long duration of bower tenure means that take-overs are comparatively rare. During the six years the populations at Taunton National Park has been studied thirty active bowers have been found and 15 bower take-overs have occurred.

In the last chapter I showed that variation in bower quality was not explained by improvements with male experience or availability in decorations. An alternative explanation is that males alter their bower display depending on the displays of their rivals. This might be expected as the relative, rather than absolute, level of male quality might be important to females in mate choice (Jang & Greenfield, 1998; Braithwaite & Barber, 2000). Bowerbird mating systems are described as "exploded leks" (Frith & Frith, 2004) and it is in "lek-like" systems, where females sample among a local group of sampling males, that relative quality may be most significant (Jang & Greenfield, 1998). There is evidence from satin bowerbirds that females do indeed sample a few neighbouring males before returning to the bower of one male to mate (Uy et al., 2000; Coleman et al., 2004).

Bower displays are perhaps unusually labile compared to other sexual signals like plumage colouration or antler size. Not only can males alter the quality of their bower during a season they can also directly influence the quality of that of their rivals', usually their neighbours', bowers by stealing bower decorations and destroying bower structures (Borgia & Gore, 1986; Borgia & Mueller, 1992; Madden et al., 2004b). There is also the possibility that "social policing" may restrict the male's level of display by "punishing" poor quality males with extravagant displays. For example, experimentally increasing the quality of bowers by adding *Solanum* berries resulted in an increased rate of destructions at supplemented bowers (Madden, 2001b; Madden, 2002). Bower owners naturally displaying a large number of berries did not suffer elevated destructions, perhaps because they were socially dominant, vigorous males, better able to deter marauders. Also, when offered additional berries, bower owners preferred to use numbers of berries similar to the number they display naturally. These results lead Madden to suggest that the number of berries displayed at the bower was condition-dependent and males were constrained by their relative quality within a population. Males that deviated from this were "punished" by their peers. Therefore, males might be able to assess their own social standing relative to their neighbours and modulate their level of display accordingly (Madden, 2002). A similar system may occur in satin bowerbirds, where blue feathers are highly prized and males continuously steal from each other. In this species younger males may display fewer feathers perhaps to reduce the threat of interference from neighbouring males (Borgia & Gore, 1986).

In this chapter I investigate possible cultural influences on bower design (Diamond, 1986, 1988). Firstly, I look at whether neighbouring males track the quality of their rivals' bowers and adjust theirs accordingly, allowing their relative display quality to remain constant (Madden, 2002; Jang & Greenfield, 1998). I look at whether within a season males track the number of decorations at their rivals' bowers. To test this I look to see whether correlations in the number of berries at bowers are stronger among individuals that are closer together. I compare the tracking of a decoration correlated with mating success (*Solanum* berries) with one that is not (*Eremophila* berries).

I then look for evidence of auxiliaries learning aspects of bower decoration (Vellenga, 1970; Maxwell as cited in Madden, 2001a). During the study 15 bower take-overs occurred: six of the new bower owners were known to be auxiliaries, three at the bower which they then went on to own and three at other bowers. I look at these birds to see if their use of bower decorations were more similar to that of the bowers at which they were auxiliaries, than were random pairs of bowers. Finally, in an experiment based around Madden and Fawcett's I consider whether males are affected by the appearance of novel objects on their own or others' bowers.

7.2 Methods

Tracking of *Solanum* berries

In 2002 and 2003, the number of *Solanum* berries displayed at each bower was counted at 10-day intervals (as described in 6.2). I tested how closely correlated each male's display (in terms of number of *Solanum* berries) was to every other male's using Pearson correlations. This generated R square values for each pair of bowers. These number of berries at each bower might be expected to correlate because of changes in environmental availability (but see 6.3) or increased collecting effort nearer to mating. To determine whether actual tracking of other's display quality might be occurring, I tested whether the number of berries on geographically close bowers were more closely correlated than those on more distant bowers. I did this using a Mantel test (Mantel nonparametric calculator, Vers. 2.0, Liedloff 1999) to compare the R square values (obtained from Pearson correlations) to geographic distribution (see 5.4). A significant negative r-value from the Mantel test would suggest that the correlation between numbers of berries is stronger at closer bowers. I compared the number of *Eremophila* berries found at each bower in the same way. In each year there was one bower owner that never used *Eremophila* berries as a decoration whose data were removed from the analyses. Ten thousand random iterations were used for each Mantel test and the input type was selected as full matrix without diagonals.

Similarity between owners and auxiliaries

The spotted bowerbird population at Taunton National Park was studied from 1998 to 2003, with the exception of 2001. Data prior to 2002 were kindly provided by Dr J. R. Madden. In each year data were collected on the number and type of decorations occurring at each bower (see 6.2 for full methods). In total there were data from 88 active bowers.

Six known auxiliary birds became bower owners. The bowers of these new bower owners were compared to the bowers where they were last observed to be auxiliaries. Not all of these birds were observed every year and there were no data from 2001, so it was not always possible to compare bowers built in consecutive years (see table 7.1)

I compared the occurrence of 92 different bower decorations at these six pairs of bowers, giving a score of one for each decoration type that was found at both bowers. I repeated this procedure for a) 24 randomly selected pairs of bower (selected from any year at any site); b) 24 pairs of bowers with the same bower owner at different years (selected randomly within owner, so that some comparisons were between consecutive years and others were not); c) 9 pairs of bowers at the same site but with different owners, who had not previously been an auxiliary at that bower.

7.3 Results

Tracking of *Solanum* berries

In 2003, the number of *Solanum* berries on nearby bowers was more strongly correlated than those on distant bowers (Mantel test: 20x20, r= -0.1476, p=0.0151). However in 2002 there was a non-significant trend in the opposite direction, more distant bowers were more closely correlated (Mantel test: 15x15, r=0.1289, p=0.0757).

In 2002, the correlation between numbers of *Eremophila* berries at bowers was stronger in more distant bowers (Mantel test: 14x14, r=0.2614, p=0.0028). However, there was no significant relationship in 2003 and the trend was in the opposite direction (Mantel test: 19x19, r=-0.0998, p=0.0827).

Similarity between owners and auxiliaries

The bowers of new owners were no more similar to the bowers where they were previously auxiliaries than pairs of bowers selected at random (two-sample t-test: t=0.14, p=0.892, see fig 7.1). There is a possible trend that the similarity is greater when the auxiliaries become owner at the same bower rather than a different one (two-sample t-test: t=-2.65, d.f. =4, p=0.057: number of matching decorations: same bower: mean ±SD = 13.67+2.31; different bower: 8.67±231, see table 7.1). There also was no similarity, beyond that of random bower pairs, among bowers at the same site but with different owners (two-sample t-test: t=0.04, d.f. =12, p= 0.968).

Bowers belonging to the same individual were more similar between years than the random pairs of bowers (two-sample t-test: t=3.06, d.f. =33, p=0.004, see fig 7.1).

Individual	Bower as auxiliary (1)	Year (1)	Bower as owner (2)	Year (2)	Number of matching decorations in bower 1 and 2
10	13	2002	2003	13	15
13	5	2000	2002	5	15
15	11	2000	2002	11	11
5	7	1998	2000	2	6
14	1	1999	2002	8	10
17	23	1999	2003	18	10

Table 7.1: The number of decorations occurring at an individual's new bower compared to the bower where it was last observed as an auxiliary, top three same bower site, bottom three at different bower sites.

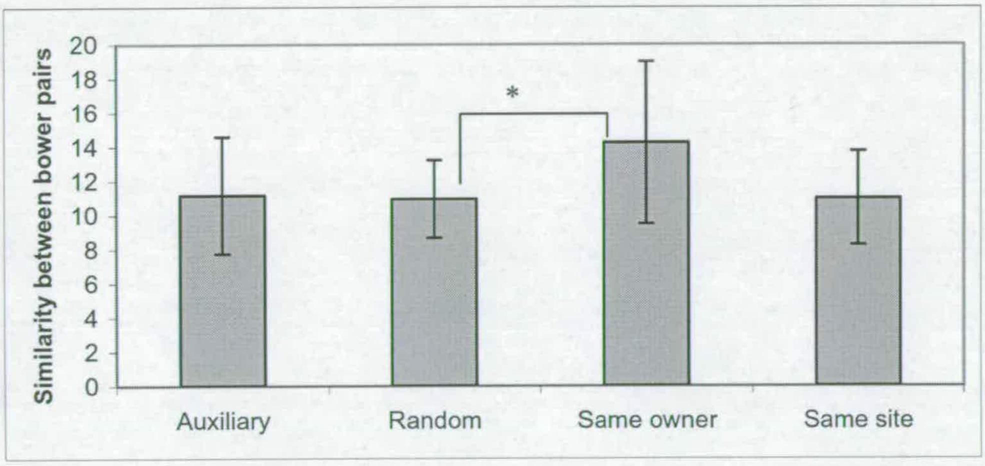


Fig 7.1: The similarity of bower decoration types in pairs of bowers. Auxiliary = auxiliary bower paired with new bower as owner; random = randomly selected bower pairs; same owner = pairs of bowers with same owner in different years; same site = pairs of bowers at the same site with different owners. Bars represent means ± SD, * = $p < 0.05$

7.4 Discussion

There was limited evidence that neighbouring bower owners track the quality of their rivals, changing their own display accordingly. In just one year, there was a significant negative correlation between the inter-bower distances and the measure of similarity (R-square) of number of *Solanum* berries at a bower. No significant relationship was found in the other year that was studied.

There was no evidence of bower owners tracking the numbers of *Eremophila* berries among bowers. Unlike *Solanum* berries this decoration type has not been shown to be a good predictor of mating success (Madden, 2001b), therefore I expected that males would not pay so much attention to the numbers at rivals' bowers nor change the number at their own bower. In one year, there was a positive correlation between bower distance and the measure of similarity of *Eremophila* berries, suggesting that males might avoid tracking the berries on nearby bowers. It is not clear what the function of this behaviour would be, unless there was some benefit of being dissimilar to neighbouring bowers.

There was no evidence from this small sample that bower owners have a similar bower design to the bower where they were auxiliary. This does not support the hypothesis that similarity among nearby bowers is due to cultural transmission. Different bower owners at the same site also do not have bowers that are more similar than randomly chosen ones suggesting the inheritance of actual bower decorations is not important in determining similarity (Pruett-Jones & Pruett-Jones, 1983). Not surprisingly, bowers built in different years by the same individual are more similar than random pairs of bowers.

It is unfortunate that data are available for only one male going from auxiliary to bower owner in consecutive years, as this is perhaps when any effect of cultural learning may be most visible. It is of note that the lack of data from consecutive years is not just due to no data from 2001. For example, individual 17, an auxiliary in 1999 and an owner in 2003, was not recorded as either an owner or an auxiliary in

2000 or 2002. It is possible that during these years the bird was an auxiliary or an owner at another, unknown, bower. Not knowing the precise histories of individual auxiliary birds makes it more difficult to know from whom they have potentially learnt their bower design.

It might be useful to concentrate any future studies of cultural transmission between owners and auxiliaries on perishable decorations, as these cannot be reused from year to year. However, I have shown that bowers at the same site but maintained by different owners are not more similar than random pairs of bowers.

As I only had a small sample of auxiliary males that later became bower owners, I used a simple comparison of the number of decorations that were similar in the different groups. It would be better, given a larger data set, to calculate similarity based on the technique described in Madden et al. (2004b). In brief, this technique is analogous to a calculation of genetic similarity. Each decoration type is equivalent to a locus at which two alternative states - comparable to alleles - exist (absent or present). This allows a similarity matrix to be compiled, giving a measure of the degree of similarity between every bower in terms of the type of decorations. These values could be used in a similar way to my measures of similarity to see if new bower owners' bowers are more similar to the bower where they were auxiliary than random pairs of bowers. This technique gives a more thorough estimate of similarity as it takes into account patterns of absence, as well as occurrence, of decorations. Even this technique is limited, because bower design is obviously more complicated than whether decorations are present or absent. Decorations can vary in number and position on the bower and the avenue walls can also vary in height, width, length and composition. Any of these features could potentially be subject to cultural learning. More detailed analyses of bower design may reveal similarities between bowers not observed here, for example seeing if auxiliaries were more likely to place particular coloured decorations on the same part of the bower.

Although patterns are contradictory between years, the possibility that male bowerbirds might be able to assess the quality of their rivals' bowers and adjust their own accordingly is intriguing (Madden, 2002). I am not aware of any studies that show individuals varying the quality of their sexual signal depending on the level of competition. Future studies to see whether males really do track the quality of rivals' bowers, could include looking at number of berries more often and over more years and also experimentally manipulating the numbers of berries at experimental bowers and looking for responses at neighbouring bowers. If individuals really do track the number of berries at each other's bowers, this might explain why neither an increase with age or in response to environmental availability was observed in the previous chapter.

In summary, I found that in one year, the number of *Solanum* berries was more closely correlated on nearby bowers than more distant ones. Although this result supports the idea that individuals track the quality of their neighbours' bowers and alter their own accordingly, a trend in the opposite direction was found in the other year studied. There was no evidence for cultural transmission of bower design from bower owners to auxiliaries as manifested when the auxiliaries become bower owners. In the following experiment I look for evidence of cultural transmission among contemporary bower owners.

7.5 Effect of exposure to novel-coloured objects on bower decoration preferences

I looked at whether bower owners were influenced by seeing novel objects at their own or rival bowers. I used an experiment similar to that of Madden and Fawcett (unpublished data; testing preference for coloured objects before and after a forced exposure) but I doubled the duration of the forced exposure to the novel objects to 28 days (30% of the total display season). No estimate of visitation rate between spotted bowerbird neighbours is available, but as stealing occurs at a rate of 0.002 per hour (Borgia & Mueller, 1992) and assuming birds are active 12 hours per day (the approximate length of daylight hours), 28 days of forced exposure would allow 0.672

stealing events to occur. As neighbouring males are often seen at each other's bowers without stealing decorations, 28 days seems a reasonable period to allow at least one visitation to neighbouring bowers during the forced exposure.

Around 92 different types of decoration were found at bowers in Taunton, the colours of which were mainly, but not exclusively red, green, white, black and silver. I chose six colours not usually found as decorations on the bowers and carried out an initial preference test. This allowed me to assess the degree of pre-existing individual variation and also to choose a colour for subsequent forced exposure. The colour for forced exposure should ideally be one that there is neither a strong pre-existing like (moved closer to the bower) nor dislike (moved further from the bower) for, and one for which the preference is similar among individuals. This gives the best chance of observing an altered preference, as if a strong dislike already exists (learnt or genetic) it may be difficult to overcome. Similarly, if the colour were already favoured, any increased preference subsequent to forced exposure would be harder to detect.

If trial-and-error learning takes place, the preference for the forced exposure colour should alter in the experimental bowers. If, however, preference for decorations were culturally transmitted the control bower owners would be expected to show a stronger preference for the forced exposure colour than initially observed in the experimental bowers. As it is possible that exposure to the counters during the first preference test might influence the second preference test, I attempted to control for this effect by carrying out the initial preference test only at the experimental bowers.

Methods

Twenty active bowers were found in 2003, 17 on Taunton National Park and three on neighbouring properties. These were divided into two groups – experimental and control – in such a way that neighbouring bowers were, where possible, in different groups (see fig 7.2).

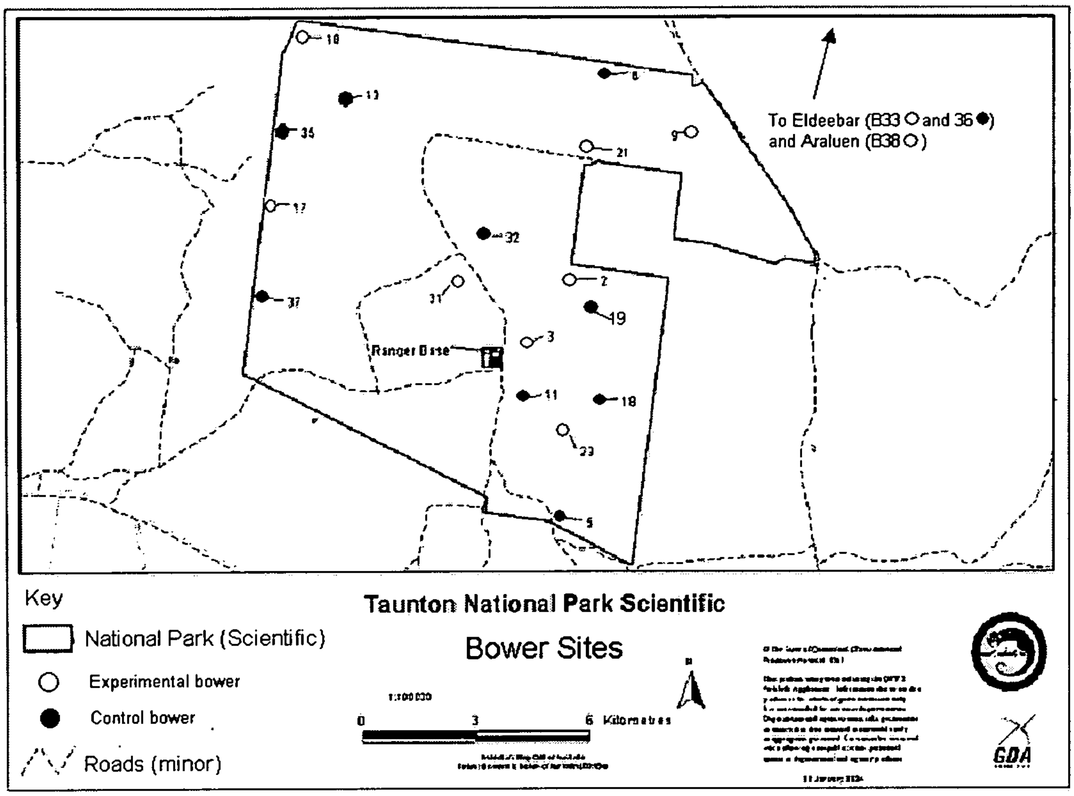


Fig 7.2: Distribution of control (black) and experimental (white) bowers on Taunton National Park

Initial Colour Preference Test

Between the 7th September and 14th September 2003 initial colour preference was tested at the experimental bowers. A pile of 30 plastic counters (5 each of gold, orange, yellow, light blue, dark blue and purple, 25 mm in diameter) was placed in a random pile on the ground 1m from the centre of the bower avenue (see fig 7.3) in the absence of the bower owner. The pile was placed at the front of the bower, defined as the side with most decorations, except when this was inaccessible or obscured from view by dense bushes. The bower was observed for 90 minutes. The time at which any counters were moved was noted and, after the observation, the precise position, measured from the centre of the avenue, was recorded. The pile was left for 48 hours to allow sufficient time for the bower owner to notice and rearrange the counters. Following this, the position of each of the counters was accurately measured from the centre of the avenue. The counters were then all removed.

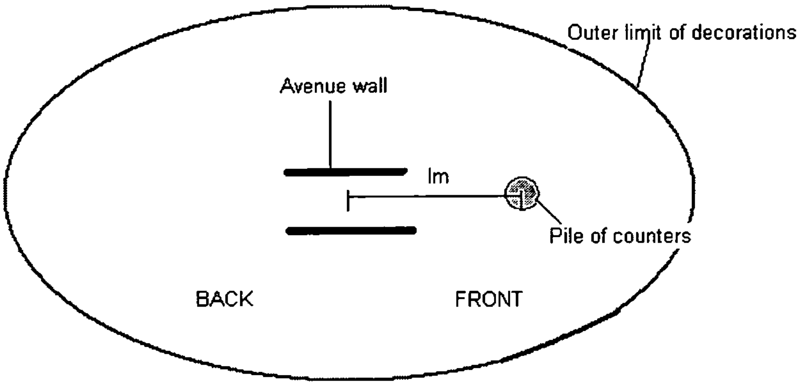


Fig 7.3: Diagram of experimental set up, viewed from above. The front of the bower is defined as the side with the most decorations, not illustrated here. The pile of counters was placed 1m in front of the centre of the avenue and the distance to the counters was subsequently measured from this same point.

Results

Initial preference test at experimental bowers

Only 14 counters were moved during the observation period at four of the experimental bowers (see table 7.2). These data were collected to give an indication of which colours were moved first but there was not sufficient rearrangement of the counters for statistical analyses.

Bower owner	Bower number	Time (mins from beginning of observation)	Colour of counter	Distance (mm from centre of ave)
2	9	79	yellow	1100
		79	yellow	1970
		79	orange	1880
		79	purple	1130
		80	light blue	1140
		80	gold	1140
12	31	4	purple	100
		4	orange	700
		5	purple	300
		5	orange	700
4	17	8	gold	220
		8	dark blue	680
		51	dark blue	620
3	10	53	gold	270

Table 7.2: Movement of coloured counters during 90-minute observation period

After 48 hours, there was significant variation in the distance different coloured counters were moved toward or away from the bower (GLM colour: $F_{5,45} = 10.52$, $p<0.001$). Individual bower owners also varied in their preference for different colours (GLM individual: $F_{9,226} = 9.14$, $p < 0.001$, individual*colour: $F_{45,226} = 2.29$, $p<0.001$). However, despite the individual variation there was a general pattern in colour preference (see fig 7.4).

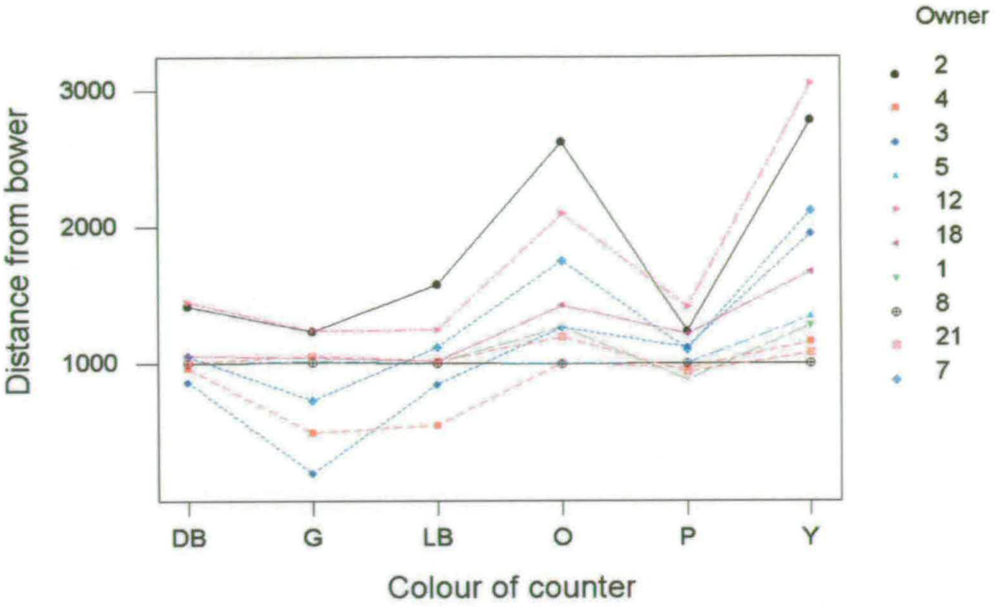


Fig 7.4: Interaction between owner and colour of counter and distance counters are moved from the bower. Points show mean distance from the centre of the bower (mm). DB=dark blue, G=gold, LB=light blue, O=orange, P=purple and Y=yellow

Yellow and orange counters were disliked by most individuals and were on average moved further from the bower. There was a range of responses to light blue and gold some individuals moved them closer to the bower and others moved them further away. Purple was chosen as the colour for the forced exposure (although dark blue would have also been a suitable choice) as least variation across birds was observed in response to purple counters and the lack of a strong preference or dislike made them suitable to look for a change in preference brought about by either trial-and-error learning or cultural transmission.

Method

Forced Exposure

Five purple counters were glued to wooden plinths (10 x 10 cm) and nailed to the centre of the avenue floor in the ten experimental bowers with one 13cm nail at each corner. Other bower decorations were moved to one side. It was necessary to attach the plinths so firmly because males would readily remove objects from the bower (J. R. Madden pers obs). Even so, one bower owner was observed to pull out a prototype plinth with shorter nails and another ripped off part of the top layer of plywood, removing three counters. Others were observed to peck violently at the purple counters. The plinths were left at these bowers between 18th September and 15th October, when they were all removed. This is a period where the bower owners are active in maintaining and displaying at their bowers and 28 days should also be sufficient for individuals at control bowers to visit their manipulated neighbours. During this period routine visits were made to the bowers (once every 5 to 8 days, mean = 6.55 days) during which I ensured the plinths and counters were still firmly attached and not obscured by other decorations.

Second Colour Preference Test

Between the 16th October and 25th October, the second preference test was carried out, on all twenty bowers, both experimental and control. As before, five of each of the coloured counters were placed a metre from the centre of the avenue (fig 7.3). They were left for 48 hours after which the position of each counter was measured from the centre of the bower.

Results

Experimental bowers

As in the initial test, there were significant main effects of individual and colour on the distance of counters from the bower (GLM individual: $F_{9,45}$=5.21, p=0.002, colour: $F_{5,45}$=2.14, p=0.007). There was no significant effect of experimental stage (i.e. prior to or after the forced exposure, $F_{1,45}$=1.90, p=0.202). However, there were significant interactions, of particular note, between the stage of experiment and colour ($F_{5,499}$=2.32, p = 0.042, see fig 7.5; also, individual*stage: $F_{9,499}$=3.02, p=0.002; individual*colour: $F_{45,499}$=2.14, p<0.001): some colours were more preferred during the first preference test whilst others were more preferred during the second. Although colour preferences changed as a result of the forced exposure, there was no change in the preference for purple counters in the initial or final preference test as measured by the mean distance the counters were moved toward or away from the bower at each bower (paired t-test: t= -0.23, n=10, p=0.820). Overall, the counters tended to be moved further away in the second preference test.

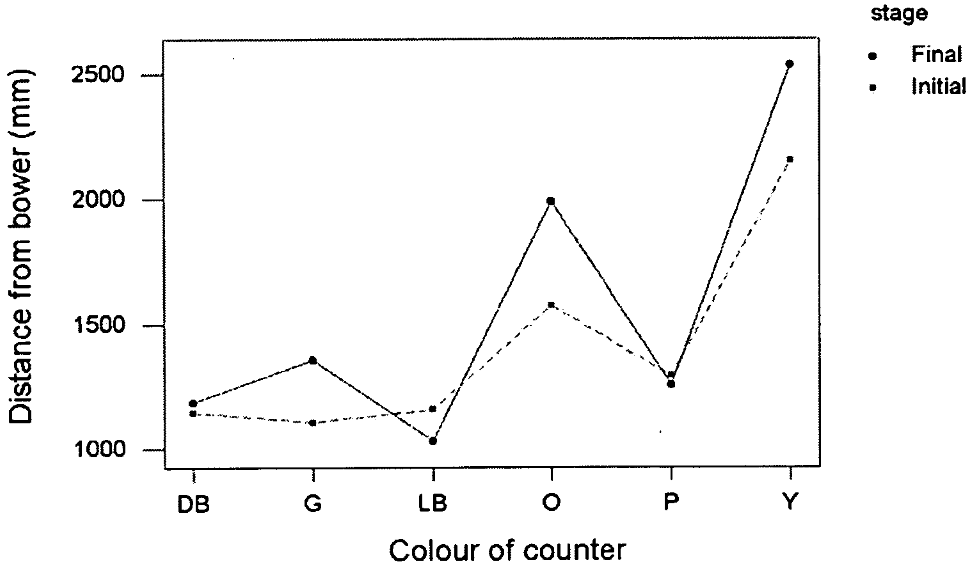


Fig 7.5: Interaction between stage of experiment, distance moved toward or away from bower and colour of counter. Points are mean distances from bower (mm). The initial preference was assessed before the forced exposure to purple counters and the final preference test immediately afterwards.

Preference test at control bowers

The data from the initial preference test at experimental bowers were compared to the preference test at control bowers. Individual bowerbirds moved counters to varying extents and the colour of the counter also influenced the distance moved toward or away from the bower (GLM individual: $F_{18,5}$=25.84, p<0.001; colour:

$F_{5,5}$=36.72, p<0.001). There was also no effect of experimental group (i.e. control or experimental) on how far the counters were moved relative to the bower ($F_{1,5}$=0.51, p=0.485 see fig 7.6). The interaction between experimental group and colour was marginally non-significant ($F_{5,547}$=2.07, p=0.067 see fig 7.6), suggesting a tendency for the preference for colours to differ to varying extents in the two groups. However, there was no difference in the mean distance of purple counters from the bower between the two experimental groups (two sample t-test: t=0.89, d.f.=14, p=0.398).

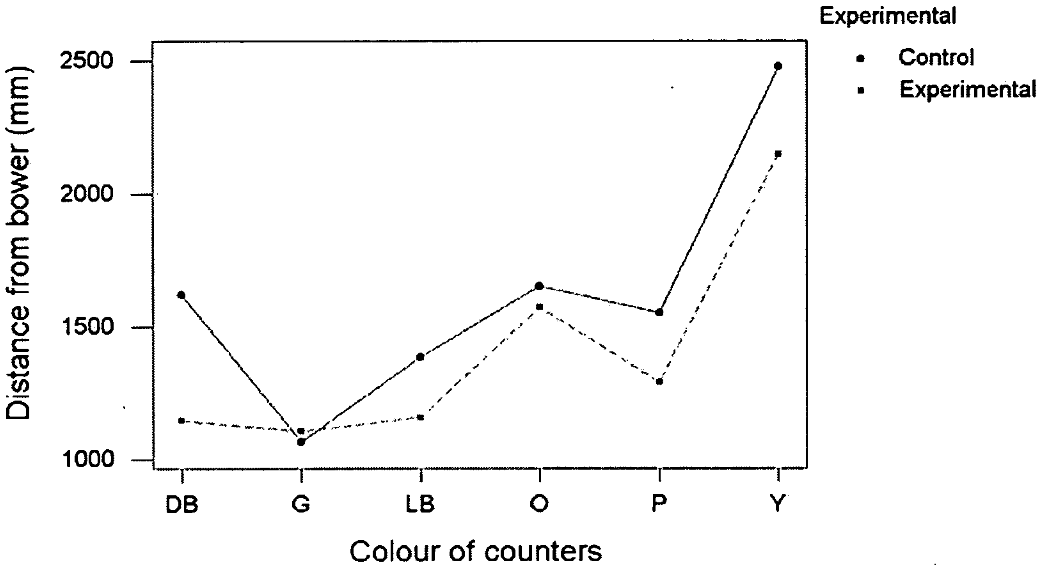


Fig 7.6: Interaction between colour and control group and experimental group prior to forced exposure. Points are mean distance from bower (mm)

I also compared the final preference at the experimental bowers with preference at the control bowers. Again, individuals moved counters varying distances and different coloured counters were moved to varying extents (GLM individual: $F_{18,5}$=17.36, p<0.001; colour: $F_{5,5}$=39.73, p<0.001). There was no difference in the distance counters were moved between the two experimental groups ($F_{1,5}$=.23, p=0.635). There was a significant interaction between experimental group and colour ($F_{5,547}$=2.92, p=0.013, see fig 7.7) suggesting that the exposure to counters has an effect on the preference of the experimental group, depending on the colour, some of which were more preferred and some less. However, with regard to the purple counters, there was no difference between the control group's preference level and that of the experimental group's (two sample t-test: t =1.02, d.f.=14, p=0.324).

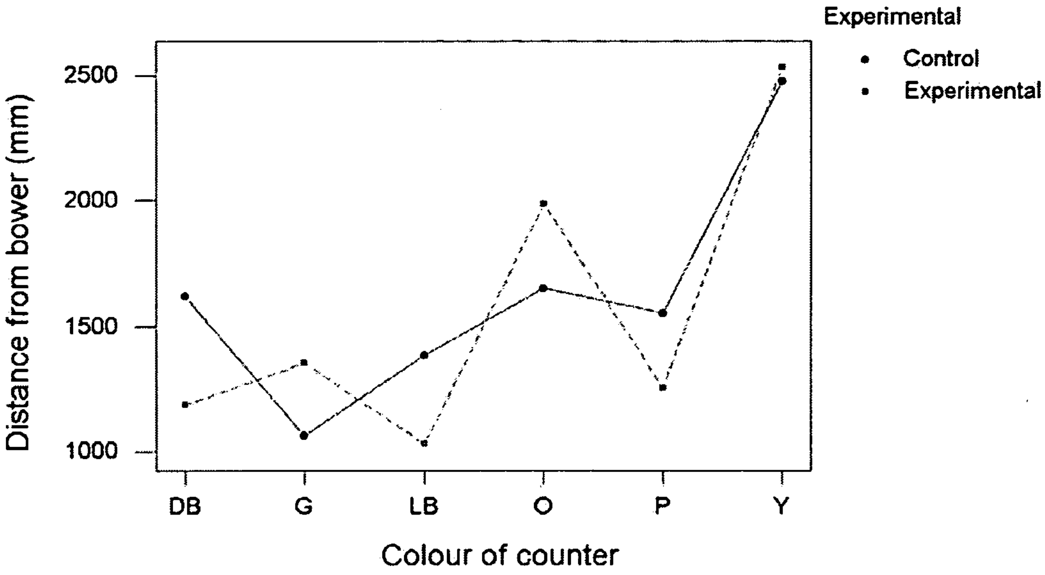


Fig 7.7: Interaction between colour of counter and control and experimental group after the forced exposure. Points are mean distance from bower (mm)

Discussion

The initial preference test confirmed that spotted bowerbirds do have pre-existing preferences for different novel-coloured objects, as measured by the distance that the birds moved differently coloured counters toward or away from the bower. These preferences varied between individuals, such that different coloured counters were moved varying extents by different bower owners and the order of colour preference also varied. However, there were similarities among individuals, for example orange and yellow counters were always left on the pile or moved further from the bower, never closer. These results, individual variation but with population-wide trends, are very similar to those found in Diamond's experiments on Vogelkop bowerbirds (Diamond, 1988).

If trial-and-error learning was occurring, experimental bower owners would be expected to alter in their preference to purple counters after seeing them on their bowers during the forced exposure. This was not observed and there was no evidence that trial-and-error learning took place. There was a significant interaction between the stage of the experiment (i.e. before or after forced exposure) and the colour of counters, there was not a change specifically in the preference for the purple counters. The previous exposure to the counters appeared to influence subsequent degree of preference for them, although not in a consistent way as some colours were moved closer and others further away. Perhaps the initial exposure reinforces pre-existing preferences for different coloured objects.

Neither was there evidence of cultural transmission among bower owners. If this were happening control males would have been expected to show a change in preference for purple counters after observing them at neighbouring bowers. There was no significant difference in the distance the counters were moved by the two experimental groups after the forced exposure suggesting that this did not effect either group's preference. Although there was an interaction between experimental group and colour, further examination revealed no difference between the distances the purple counters were moved. The reason other colours were moved varying amounts between the two groups is not entirely clear. It may be as mentioned above that exposure during the initial preference test in the experimental bowers strengthens existing likes and dislikes of various coloured objects. However, there was also a marginally non-significant interaction between group and colour when comparing the initial preference test with the test at the control bowers, suggesting there may have been pre-existing differences between the two groups, not caused by the experimental procedure.

The inconclusive results might be due to problems in experimental design. Most importantly, the lack of an initial preference test at the control bowers prevented any measure of a change in preference in this group. If there had have been a strong effect of cultural transmission this might have still been evident as a significant difference in the distance purple counters were moved between the initial preference test at the experimental bowers and the only preference test at the control bowers. It would have been unlikely, although not inconceivable, that the control group had a pre-existing preference for purple counters that differed significantly from that of the experimental group. However, no such obvious effect was found and the potential individual differences limit the conclusions that can be drawn. It would have been better to treat the groups exactly the same except for the controlled exposure. Any difference in response to the purple counters, beyond that of other colours, could then be attributed to trial-and–error learning at the experimental bowers or cultural transmission at the control bowers. It should also be noted that these two hypotheses are not mutually exclusive and it may be more difficult to decipher the results if both types of learning are occurring.

Additionally, not all of the counters were moved from the initial pile, which might mean the bowerbirds either did not notice them or that they were completely indifferent to their presence. The counters were placed one metre from the bower because this fell within the radius of naturally occurring decorations but allowed the owner to move the counters either closer to the bower (indicating a preference) or further away (indicating a dislike). Some other similar experiments (e.g. Diamond, 1986; Diamond, 1988) have placed experimental decorations in the avenue (or equivalent structure in maypole bowers), which may produce a stronger effect (see below) but it would be harder to differentiate between tolerating a decoration on the avenue rather than actively preferring it.

I assumed that the nearer a counter was moved to the centre bower the more preferred it is. This is based on observations that preferred decorations are more often displayed in the central avenue and disliked objects can be moved up to 10m from the bower (Madden, 2003a; see also Diamond 1986). However, this assumption might be flawed. Some decorations are always or nearly always displayed outside the centre of the avenue (e.g. snail shells and itchy grub cases). These are presumably not disliked as decorations as they were chosen and collected by the bowerbird, however the preferred position for these objects is outside of the avenue.

Further, carefully designed experiments are required to find the cause of the spatial similarity of spotted bowerbird bowers (Madden et al., 2004c). For example, very little is known about the rate and duration of female visits to the bowers. To show trial-and-error learning is occurring it might help to know more about the female preferences and how these might be conveyed to the males. However, any experiments are complicated by the number and diversity of decorations found at spotted bowerbird bowers. It is impossible to know what prior exposure birds may have had to objects and colours, especially as all the owners of all the bowers studied here incorporated man-made objects. It would perhaps be beneficial to study cultural influences in captive bowerbirds where their exposure to experimental objects could be more carefully controlled.

The results of this experiment, like those of Madden and Fawcett (unpublished data) do not provide evidence for cultural transmission of preferences for bower decorations. There was no evidence that the preferences of experimental bower owners were influenced by the presence of purple counters at their bowers (trial-and-error learning). Nor was there evidence of a cultural transmission of a preference for purple counters after control males observed them at neighbouring bowers.

7.6 General discussion

There are between population variations in spotted bowerbird bower design (Borgia & Mueller cf. Madden, 2001b) and within the Taunton population there are fine scale patterns (Madden et al., 2004c) that are consistent with either cultural transmission among neighbouring bower owners or a response to localised female preferences (Diamond, 1986). Males might also be aware of their own and their neighbours' social status and retain the same relative quality by tracking changes in decoration over the season and punishing males that display more preferred decorations than their status permits (Madden, 2001b; Madden, 2002). It seems, then, that spotted bowerbirds acquire information via cultural transmission in their sexual displays.

However, my data provide very little support for the importance of cultural influences on bower design. There is a possibility that males track the number of *Solanum* berries on nearby neighbours' bowers but this was only observed in one of the two years data. There was no evidence of cultural transmission of bower design between bower owners and auxiliaries. Finally, forced exposure of a novel object did not provide any evidence of trial-and-error learning or cultural transmission. Although my results do not support cultural transmission in bowerbirds, it cannot be completely ruled out.

Chapter 8. Discussion

8.1 Function of vocal mimicry in the spotted bowerbird

In my introduction I discussed four main hypotheses that might explain the function of vocal mimicry in spotted bowerbirds, as well as in other species. I now revisit those hypotheses and summarise my findings from experimental and observational studies and suggest some areas for further work.

1) Interspecific communication – avoidance of threats and/or competitors

Firstly, vocal mimicry might serve an interspecific function, allowing mimics to avoid threats or competitors. Several hypotheses have been suggested in this category, and I considered two with respect to bowerbirds: the Beau Geste hypothesis (Rechten, 1978) and the Batesian acoustic mimicry hypothesis (Dobkin, 1979). I did not specifically address the third hypothesis that vocal mimicry causes an intervention by another species (either secondary predator or heterospecific that might mob a predator; Morton, 1975; Chu, 2001b; Chu, 2001a). However, I never observed mimicry attracting other heterospecifics, which might have been expected when simulating predatory attacks at the bower (chapter 4 as in Morton, 1976). It might be of significance that the three birds observed mobbing the brown falcon mount during the presentation experiment, (apostlebird *Struthidea cinerea*, noisy miner *Manorina melanocephala* and pied butcherbird *Cracticus nigrogularis*, chapter 4), are also mimicked by the bowerbird. Their presence and subsequent mobbing was not preceded by bowerbird mimicry. However, to completely exclude this hypothesis as an explanation, one would need to determine the context in which calls are used in by the model and whether the model species respond to mimicry of these calls (Baylis, 1982; Chu, 2001a).

The Beau Geste hypothesis suggests that mimics deter their competitors by making the environment sound more crowded than it really is. If mimetic vocalisation fulfills this function, the mimic should copy competitor species preferentially and also mimic in their presence. The spotted bowerbirds in my study did neither of these: they did not preferentially mimic other frugivores, nor did the rate of mimicry increase in the presence of competitors (chapter 3). Hence, this function of mimicry is unlikely in this species.

The Batesian acoustic mimicry hypothesis suggests that mimics deter predators or competitors by mimicking aggressive species. Competitive Batesian acoustic mimicry (Dobkin, 1979) seems unlikely in the spotted bowerbird because, as mentioned above, mimetic rate does not increase in the presence of competitors. However, there are several lines of evidence that suggest that spotted bowerbird mimicry might be used to deter predators. Firstly, aggressive species made up a disproportionate number of bowerbird models (chapter 3). Secondly, the rate of mimetic vocalisation tended to increase in the presence of threatening species (chapter 3). Thirdly, human disturbances at the bower caused an increase in mimetic rate (chapter 4). Finally, the tendency of birds to either remain near the bower and mimic, or to fly off silently, in response to human disturbances suggested that the "predator" might be the intended receiver (chapter 4).

Not all of my data, however, fit the predictions of the Batesian acoustic mimicry hypothesis. Bowerbirds did not respond with mimicry to the presence of a mount of a known predator (brown falcon) and more than half the birds tested did not respond to disturbances at the bower with an increase in mimetic vocalisation (chapter 4). Furthermore, not all mimicked calls were of aggressive species (chapter 3). However, it is perhaps not necessary to mimic aggressive species to gain the advantage of Batesian mimicry, and other unpalatable or non-profitable models could be copied.

The context in which calls are made by the model might provide information about their function in the mimic (Baylis, 1982). I did not look at this specifically, but I noticed that two of the calls mimicked by spotted bowerbirds appeared to be used by their models when threatened. The rattling alarm call of a willie wagtail (*Rhipidura leucophrys*, Simpson & Day, 1999) was heard when a nesting bird was disturbed and the "eerik" call of a pied butcherbird (*Cracticus nigrogularis*) was used by the model species in response to the mount of the brown falcon and also to human disturbance. As noted above, the three species that mobbed the falcon mount are also mimicked by the bowerbird. Perhaps instead of copying aggressive species bowerbirds could mimic unprofitable prey, which could include species that mob as well as non-prey species, like other predators. It is possible that the threat of being mobbed is sufficient to deter a predator from attacking. I have not observed, or read of, mobbing behaviour in bowerbirds, suggesting a possible need to mimic mobbing species rather than producing species-specific calls. There was also a possible tendency to mimic group living birds (e.g. fairy wrens *Malarus* spp, apostlebirds *Struthidea cinerea* and babblers *Pomatostomus temporalis*). Perhaps these are also unprofitable prey because of confusion effects or mobbing behaviour by other group members (Krebs & Davies, 1987). Mimicry of mobbing or group-living species could still be considered a type of Batesian mimicry as a "palatable" prey item (the bowerbird) mimics "non-palatable" (or non-profitable) prey items. The bowerbird might also be expected to vary which species it mimics depending on the nature of the predator.

Although I have shown that spotted bowerbirds preferentially mimic aggressive species and tend to mimic in response to potential threats (naturally occurring ones and human induced ones), to conclusively show that spotted bowerbird mimicry is a type of Batesian acoustic mimicry, the reaction of the intended receivers – potential predators – also needs to be tested. Mimetic vocalisation must have an effect on the predator: startling, confusing or otherwise deterring or impeding their attack (Vernon, 1973; Curio, 1978). As predation events are too sporadic and unpredictable to rely on observing naturally occurring ones, an experiment should be set up to test the reaction of predators to mimicry. Perhaps a bowerbird mount could be accompanied with playback of either species-specific or mimetic calls and the approach rate of predatory species could be compared. Even this would be logistically difficult, as it would require the presence of predatory species and for them to be sufficiently deceived by a mount to consider attack. It might be possible to test reactions of captive raptors to playback of modelled and mimicked calls to see if they are able to distinguish between them (Chu, 2001a). This would at least demonstrate whether predators are potentially deceived by mimicry, although would not allow assessment of how they would react to mimicked calls during a hunt. Studying the mimicry of nesting female spotted bowerbirds could also be illuminating (Chisholm, 1937; Warham, 1962; Frith & Frith, 2004). Attempted nest predation events are perhaps more frequent than attacks on adult bowerbirds and at least occur at a predictable location: this might permit observation on whether attacks are less likely to be successful if the female employs mimicry. However, ethical and logistical considerations make the testing of hypotheses involving predation very difficult.

2) Sexual selection

An alternative hypothesis was that mimicry is incorporated into song to increase repertoire size, a trait that is often shown to correlate with female preference (Eens et al., 1991; Mountjoy & Lemon, 1996) and mating success (Hiebert et al., 1989). Unlike many other bowerbird species (Frith & Frith, 1993, 2000; Frith & McGuire, 1996), spotted bowerbirds do not include mimicry in their courtship displays. This does not rule out a sexual function for mimicry but the interpretation of my data suggests that it is unlikely.

Firstly, spotted bowerbirds do not increase the rate of mimetic vocalisation in the presence of conspecifics as might be expected if mimicry was important in sexual selection (chapter 3). However, I do not know if the rate changes in the presence of female conspecifics as no ringed females were observed during the course of my observations. More females could be ringed in future studies to see if male mimicry rate changes in their presence and also to observe female use of mimicry.

Secondly, I did not observe an increase in repertoire size with bower tenure, although there was a tendency for bower owners to have larger repertoires than auxiliaries (chapter 5). In some species, species-specific repertoire is added to over time (Nottebohm & Nottebohm, 1978) and is therefore an honest indicator of male age. Although I observed variations in individuals' repertoires over the two years, there was, if anything, a decrease in repertoire size in the second year (chapter 5). Previous studies on captive birds (Laskey, 1944; Kaplan, 1999) have shown that new mimetic calls can be added throughout life. However, I believe my study to be the first to look at mimetic repertoire in wild birds over two years, and I am certainly not aware of any longer-term studies. Longitudinal data would show whether new calls are added and others lost over time, providing information on both the possible function and the acquisition of mimicry.

Thirdly, there were no relationships between vocal characteristics, such as rate of species-specific vocalisation and repertoire size, and measures of bower quality previously shown to correlate with mating success (chapter 6). Although different measures of male quality that are used as indicators by females might be expected to be correlated (Johnstone, 1995; Doucet & Montgomerie, 2003), there is a lack of consensus among theoretical studies as to whether this is the case (Moller & Pomiankowski, 1993; Johnstone, 1995). Therefore the lack of correlation between vocal and bower characteristics cannot be used to definitively rule out the use of vocal traits in sexual selection.

Finally, if mimicked calls are used in mate choice or male-male competition, there might be selection for calls that are expensive to produce (Gibson & Bradbury, 1985; Gil & Gahr, 2002). This appears to be the case for species-specific calls, for example female swamp sparrows (*Melospiza georgiana*) prefer males with high trill rates, which are energetically costly (Ballentine et al., 2004). There was no evidence that spotted bowerbirds were preferentially mimicking complex or rare calls (chapter 3), which could be favoured due to difficulty of learning or female preference for novelty (ten Cate & Bateson, 1988).

The only evidence that suggested mimicry might be involved in sexual selection was an increase in the occurrence of mimicry as the season progressed towards breeding in 2002 (chapter 3). This would be consistent with mimicry being used more often when males are trying to attract females, as is seen in species specific vocalisation of starlings (*Sturnus vulgaris*, Cuthill & Hindmarsh, 1985; Eens et al., 1993). However, the same pattern was not found in the second year of the present study, perhaps due to a later start in the field season, there was no change in mimetic rate. Taking these results together, it seems unlikely that that mimicry has a substantial influence on mating success.

It would be useful to completely exclude this hypothesis by looking for a relationship between vocal characteristics and mating success in the same individual in the same year. Motion-sensitive video cameras could be used to film copulations (Borgia, 1985b; Madden, 2001b) or to record other measures that might correlate with female preference, like duration of (ringed) female visits (Lenz, 1994). Other vocal traits, not measured here, might be more likely to correlate with mating success, in particular the quality of mimetic calls. Loffredo and Borgia (1986) found that the structural integrity of mimicry was age-related and correlated with mating success but neither this nor any other study, has looked at the accuracy of the mimicry when compared to the model species. This could be done using cross-correlation techniques (Feekes, 1982; Clark et al., 1987; Hile et al., 2000). More accurate mimetic renditions might indicate better quality mates. Alternatively, there might not be selection for accuracy in calls used in sexual display due to the need for species recognition (Rechten, 1978; Dobkin, 1979).

3) Social affiliations

Mimicry may also play a role in social affiliations other than during courtship. There are several different ways this might occur. Firstly, mimetic calls might be used in individual recognition (Harcus, 1977; Feekes, 1982). The lack of increase in mimetic calls in the presence of conspecifics might suggest this is unlikely to occur in spotted bowerbirds, but even more compelling evidence is the rarity of their use of vocal mimicry. Estimations of complete repertoire size reveal that, even when I observed an individual bowerbird for over 10 hours, I did not always capture the complete repertoire (chapter 5). Whilst it might not be necessary for a conspecific receiver to hear the entire repertoire, it seems likely that hearing a substantial proportion of it would be necessary to distinguish individuals. On the other hand, in 2002 there was a tendency for geographically close bower owners to share less mimicry than more distant birds, which could represent active avoidance of the same mimicry type, as found in starlings (chapter 5, Hausberger et al., 1991). The need for individual recognition in bowerbirds is not obvious, except perhaps to avoid unnecessary agonistic interactions in feeding flocks (Collis & Borgia, 1992) or inbreeding (Emlen, 1997). During the period of bower maintenance individual males can often be associated with their presence at a particular bower location and this might be more useful than knowledge of rivals' or potential mates' mimetic repertoires.

The second social use of mimicry has been termed "phatic communication". This type of mimicry allows lyrebirds (*Menura* spp.) to maintain contact with conspecifics without signalling alarm, threat or reproductive status as would be conveyed by species-specific vocalisations (Robinson, 1991). Whilst I did not explicitly test the birds in such a way as to determine if this function explains vocal mimicry in spotted bowerbirds, it seems unlikely as they lack the social cohesion of lyrebirds. However, the use of mimicry for phatic communication during wintering feeding flocks when birds form groups of around 10 to 30 (Frith & Frith, 2004) cannot be excluded.

Finally, mimicry might be used in matched counter-singing (Harcus, 1977; Catchpole & Slater, 1995). If this were the case neighbouring males would be expected to have a higher number of shared songs compared to more distant individuals. The opposite relationship was observed in bowerbirds (chapter 5). It is also unlikely that spotted bowerbirds' comparatively quiet mimicry would be transmitted the distance of a kilometre or more to a rival male's bower.

The social affiliation hypotheses for vocal mimicry, therefore, seem unlikely to apply to bowerbirds, unless mimicry is used in social interactions away from the bower, for instance, at feeding sites.

4) Learning Mistakes hypothesis

The Learning Mistakes hypothesis suggests that mimicry is a non-functional by-product of the ability to learn species-specific vocalisation (Hindmarsh, 1986). As such, mimicked calls would be expected to be common in the sound environment and simple or similar to the mimics' own calls. If mimicry had no function beyond that of species-specific vocalisation, it would also be expected to occur at the same rate and in the same context as species-specific calls. None of the data I collected support the predictions from this hypothesis. Firstly, spotted bowerbirds do not preferentially mimic the most commonly heard calls in the sound environment, either on the scale of the National Park or those heard around their bower (chapter 3 and 5). Secondly, there is no tendency to copy calls with the simplest acoustic structure (chapter 3). Thirdly, bowerbirds do not mimic calls that share the same acoustic structure as the species-specific hiss, although there was a non-significant tendency to mimic calls with a similar amplitude modulation (chapter 3). Finally, there was a negative correlation between species-specific and mimetic vocalisation (chapter 3 and 4), suggesting the two types are used in different contexts and might, therefore, serve different functions.

Although I have no evidence for the Learning Mistakes hypothesis, I might not be able to exclude it entirely as an explanation of bowerbird mimicry because of limitations in my methodology. In particular, my methods for looking at the simplicity and similarity of mimicked and model calls could be improved. I used the same system as Hindmarsh (1984), rating calls according to the complexity of their frequency modulation, frequency structure and amplitude modulation. However this system is perhaps slightly anthropocentric and does not necessarily reflect what is a complex sound for a bird to produce. The alternative would be to look at the actual cost of producing particular types of sound, perhaps in terms of oxygen consumption during mimetic versus species-specific calling (Gil & Gahr, 2002). Limitations imposed by a species' vocal tract and bill morphology might influence which models can be mimicked. For example, birds with large beaks and body size might be restricted to comparatively low rates and frequency bandwidths (Podos, 2001; Podos et al., 2003). These limitations should be taken into account when assessing whether commonly heard songs are mimicked more often, and the calls that are beyond the species-specific range of the mimic should perhaps be excluded. Principle component analysis could be used to assess whether many different measures of acoustic structure (i.e. frequency bandwidth, maximum frequency, number of frequency inflections and so on) are more likely to be shared among the mimic's species-specific calls and actual, rather than potential, models (Hamao & Eda-Fujiwara, 2004). This provides a more objective way of measuring similarity between calls than visual inspection of sonograms. Other than Hindmarsh's work (Hindmarsh, 1984, 1986) no study has addressed the way in which the structure of mimicked call relates to the structure of species-specific vocalisation. This might be useful in determining the function of mimicry in various species. For example, species that have been shown not to mimic common calls preferentially (including spotted bowerbirds; phainopeplas, Chu 2001b; robin chats, Ferguson et al., 2002) might actually turn out to do so once calls that are beyond the limits of their vocal apparatus are excluded, this would then be consistent with the Learning Mistakes hypothesis.

Mimicry due to mistakes made during song learning is only a relevant hypothesis if bowerbirds do learn their species-specific vocalisations. Oscines, like bowerbirds, usually learn their song (Brenowitz, 1982) but there is evidence that simpler calls are innate (McGregor et al., 1991; ten Cate et al., 2002). It would be informative to rear bowerbirds, isolated from conspecifics or deafened (Konishi, 1965) to see whether their characteristic hiss calls require learning and/or social reinforcement. If species-specific calls were unlearnt it would exclude the Learning Mistakes hypothesis for mimetic vocalisation.

In summary, the interpretation of my data provides mixed support for the Batesian mimicry hypothesis and I cannot entirely rule out any of the other hypotheses, although it should be noted that they are not necessarily mutually exclusive. For example, preferred males might also be the best at deterring predators with their mimicry. At this point the data are more consistent with the predictions from the Batesian mimicry hypothesis than any of the others and thus this hypothesis is, currently, the most likely explanation for mimicry in the spotted bowerbird. My data are also, to my knowledge, the first experimental support of this hypothesis.

8.2 Function of species-specific calls

I collected data on species-specific hiss calls as a useful comparison to mimetic calls, for example, to see if species-specific rate was correlated with mimicry rate, which might indicate that the two types of calls serve a similar function. I found some evidence that species-specific calls, unlike mimetic ones, are used in intraspecific communication and possibly serve a sexual function. There was no change in the rate of species-specific hiss in the natural presence of competitor or aggressive species (chapter 3) but there was a possible increase in rate in the presence of conspecifics (chapter 3). The rate of species-specific vocalisation increased towards the mating season in 2003, suggesting it might have been used in sexual selection, at least in that year (chapter 3). There was no obvious change in rate of hiss with length of tenure but auxiliaries hissed at a higher rate than did bower owners (chapter 5). Borgia and Presgraves (1998) found that the ratio of long to short hisses was important in determining mating success, the rate of mimicry could be too. It would be interesting to determine whether the relationship between hiss length and mating success is also found in the Taunton population.

Species-specific vocalisation rate also tended to increase in response to the mount of the brown falcon during the presentation experiment, suggesting that species-specific hisses are used when threatened (chapter 4). The falcon, as a known predator of bowerbirds (J. R. Madden, pers comms) represents an obvious threat. However, the rate of species-specific vocalisation did not alter during the disturbance experiment (chapter 4) suggesting that it is not always used when the birds are threatened.

Spotted bowerbirds also make a series of "mechanical" noises: gurgles, buzzes and bill clicks (Frith & Frith, 2004). I have not considered the function of these species-specific vocalisations in detail because these were often very quiet and so were not always audible on recordings. The advertisement call, which consists of a series of loud hisses usually produced from a vantage point, might be used to advertise the location of the bower and/or the rate of attendance to rivals and/or females. There was no evidence of it being used as perception advertisement during the presentation experiment (chapter 4, Curio, 1978; Rainey et al., 2004).

8.3 Acquisition of mimicry in spotted bowerbirds

My study provided no circumstantial evidence of mimicry being learnt from conspecifics. Neighbouring bower owners did not share more mimicked calls than more widely dispersed individuals (and in fact the reverse might be true) and there was no evidence of related birds sharing mimicked calls (chapter 5). I did not test the alternative theory, that mimicry is learnt directly from heterospecifics.

The acquisition of mimicry could be addressed more thoroughly by future studies. In particular, transmission of mimicked calls among adult bowerbirds could be tested by looking at the similarity of shared mimicry, rather than just the number of calls shared. For example, cross-correlational techniques (Feekes, 1982; Clark et al., 1987; Hile et al., 2000) could be used to quantify whether the calls of nearby bower owners are more similar than distant ones and are therefore acquired by copying conspecifics. Another potential source of transmission is from the mother to offspring. Recording the mimicry of the nesting female and comparing it to the mimicry of her adult offspring (recognised by ringing) would be extremely labourintensive but could provide evidence for transmission of mimicry among individuals. As suggested above, rearing bowerbirds in captivity would allow carefully controlled tests (e.g. using playback) to ascertain what type of sounds are mimicked and under what contexts (Marler & Peters, 1977; Baptista & Morton, 1981; Baptista & Petrinovich, 1984). There might be evidence from existing collections of captive bowerbirds as to whether individuals can add to their repertoire throughout life, perhaps after the addition of a new species to an aviary, as has been shown in mockingbirds (Laskey, 1944) and Australian magpies (Kaplan, 1999). This would demonstrate that learning mimicry is open-ended (Nottebohm & Nottebohm, 1978).

8.4 Techniques for studying vocal mimicry

My results would have been more easily repeatable if I had used an objective measure of what constitutes mimicry, rather than simple visual and acoustic inspection of sonograms and recordings (Baylis, 1982). For example, Hamao and Eda-Fujiwara (2004) measured five different parameters from sonograms of model calls and suspected mimicry (identified by visual inspection of sonograms) and used Principle Component Analysis to compare the similarity of the two sets of calls. The first and second principle components were plotted against each other and only calls that fell within the boundaries of the model call parameters were considered to be mimicry. Using this technique, only 57% of suspected mimicry was confirmed as such. Whilst this might produce overly conservative results, it highlights the potential ambiguity of identification of mimicry in the absence of quantitative criteria. I was prevented from using this or other, cross-correlation techniques (e.g. Feekes, 1982; Clark et al., 1987; Hile et al., 2000), due to the lack of recordings of the calls of models. Several model calls from different individuals need to be recorded to gain call parameters that are truly representative of the species, otherwise the occurrence of mimicry could be further underestimated.

As different observers identifying the same sonograms by eye may reach different conclusions (Jones et al., 2001), I attempted to investigate this variation in objectivity by calculating inter-observer reliability scores for my visual classification of sonograms (chapter 2, Jones et al., 2001). Here I tested whether volunteers matched mimicked calls with the same model calls as I did. The test was limited as I could not ask volunteers to match mimicry to any potentially mimicked call (i.e. any call heard in the sound environment) and they were restricted to visual inspection whereas I combined this with listening to the calls. However, I am satisfied that it demonstrated a degree of confidence in my analyses that would allow other observers to reach the same broad conclusions about bowerbird mimicry. Other studies have sought confirmation of identification of vocal mimicry from experienced ornithologists familiar with the models' calls (Cruickshank et al., 1993; Ferguson et al., 2002) but many studies on mimicry (and also more generally on bird song) do not appear to address the issue of reliability of classification at all (Jones et al., 2001).

I believe my use of the capture-recapture technique to estimate repertoire size (Garamszegi et al., 2002, 2005) to be the first time this technique has been applied to mimicry. The technique allows an estimate of the complete mimetic repertoire for individuals taking into account the heterogeneity of call production. Although it produced reasonable estimates of individual mimetic repertoire size (especially when compared to the traditional asymptotic technique, Howard, 1974), there were potential problems. There were biological difficulties in the definition of a mimetic call and bout, and also analytical ones, like the ability of the estimation technique to deal with small sample sizes, both in terms of the size of the repertoire and the number of mimetic bouts. The definition of different units of species-specific song, whilst perhaps not having reached a stage of complete consensus in the literature, is frequently discussed (e.g. Catchpole & Slater, 1995). By comparison there is inadequate discussion of what constitutes a mimetic call, bout and so on. I believe my definitions to be biologically useful but unless consistent terms are used by everyone working on vocal mimicry, comparison among species will be hampered (Dobkin, 1979). Further work on estimated and observed mimetic repertoire sizes is also required in other species to test the ability of capture-recapture techniques to deal with small repertoire sizes encountered in mimicry.

8.5 Bowers and bower quality

It is impossible when working on bowerbirds not to be impressed by the bower structure itself and the length of time males' spend maintaining it and arranging decorations. Although far more is known about the function of spotted bowerbirds' bowers than its vocalisation (e.g. Borgia, 1985b; Madden 2001b; Uy & Borgia, 2000), there are still gaps in out knowledge. For example, it has been suggested that bowerbirds learn how to build their bowers from observing other males (Vellenga, 1970; Borgia, 1993; Maxwell et al., 2004) and that cultural transmission might explain the similarity in geographically close bowers (Madden et al., 2004c). However, no studies have provided clear evidence for learning or cultural transmission and I found none in my data either.

Bowers belonging to younger males are often poorly constructed (Pruett-Jones & Pruett-Jones, 1983; Diamond, 1986; Frith & Frith, 2004) and the bowers of juvenile males brought into adult condition with testosterone implants are worse than experienced males (Collis & Borgia, 1993) but no one has tested whether the quality of individuals' bowers improves with age. I examined data for up to six years of bower tenure but found no evidence of bowers improving (chapter 6). There was a negative correlation between the total number of decorations and the duration of bower tenure, which, as number of decorations is correlated with mating success (Borgia, 1985b, 1995a; Hunter & Dwyer, 1997), suggests bower quality actually decreases.

Madden (2001b) found that the number of *Solanum* berries displayed on the bower was the best predictor of mating success. Artificially elevating the number of berries displayed at bowers resulted in increased destructions by rivals whilst the same was not observed at bowers with naturally high numbers of berries (Madden, 2002). These observations lead to the suggestion that males displayed according to their status, and inferior males presenting high quality displays were "punished" by their peers. This requires males to be able to assess their own social standing relative to their neighbours, hence they might track the quality of rivals' bowers and adjust their own accordingly. I found some evidence suggestive of males tracking the number of *Solanum* berries at neighbours' bowers. In 2003, the numbers of berries at nearby bowers were more closely correlated across the season than at more distant bowers, (chapter 7) and the number of berries was not explained by fluctuations in environmental availability (chapter 6). The intriguing possibility of tracking rivals' display quality could be tested by increasing the number of berries on some bowers and seeing whether their neighbours' increase the number of berries to retain the same relative level of quality.

The similarity of nearby bowers, in terms of type of decoration could be explained by cultural learning (Madden et al., 2004c), however I found no evidence of this either between owners and auxiliaries, or among contemporary bower owners (chapter 7). Forced exposure to a novel decoration at the bower did not appear to bring about changes in preference for that decoration either by trial-and-error learning, where the bower display is influenced by localised female preference, or by cultural transmission among bower owners (Diamond, 1986; 1988). Further experiments are required to explain how local traditions in bower designs arise, in particular, how female preferences are conveyed to the male. For instance, by seeing if duration of female visits to bowers change depending on the number of preferred objects. Any experiment looking for cultural transmission in wild birds might be restricted because prior experience to objects and colours cannot be controlled, and for this reason studying captive individuals' (both female and male) preferences could be beneficial (Madden & Tanner, 2003).

In agreement with previous studies (Borgia, 1985b, 1995a), I found that some measures of bower quality do correlate with each other (chapter 6). However, I did not find correlations between bower quality and vocal characteristics. This might reflect a lack of correlation between different aspects of a multi-component signal

(Johnstone, 1995; Johnstone, 1997; Rowe & Skelhorn, 2004). The alternative interpretation is that the vocal characteristics measured do not function as indicators of male quality. This is consistent with other evidence that mimetic vocalisation is not sexually selected. That is, mimetic rate does not increase in the presence of conspecifics and repertoire size does not appear to increase with tenure. However, rates of *species-specific* vocalisation did not correlate with bower quality either, the rate of which does tend to increase in the presence of conspecifics and increase the breeding season. A definite link between vocal characteristics and mating success should be demonstrated before conclusions are drawn about the lack of correlation among potential components of a multiple signal display (e.g. Doucet & Montgomerie, 2003).

8.6 Conclusions

During the course of this thesis, I have gone some way to address Dobkin's (1979) "appalling lack of experimental verification" of vocal mimicry, in one example of a proficient mimic, the spotted bowerbird. Whilst the evidence is not conclusive, I have shown that the function of vocal mimicry in this species is unlikely to be explained by mistakes made during learning, sexual selection or social affiliation. Instead it appears to perform an interspecific role, potentially as type of Batesian acoustic mimicry. There is individual variation in the rate of mimicry and repertoire size but there was no obvious correlation with age. Vocal traits were not observed to correlate with measures of bower quality. There was no evidence that mimicry was learnt from neighbouring or related conspecifics or directly from models. This is the first study that presents any experimental evidence for Batesian acoustic mimicry, it would therefore be especially useful to confirm whether this is the real function of spotted bowerbird mimicry. Future studies could address this by observing the response of potential receivers (predators) to determine whether mimetic vocalisation is effective in deterring or decreasing their success in attacks on spotted bowerbirds.

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Appendix

A.1. Examples of mimicry

On the following pages are examples of spectrograms showing the visual resemblance between model calls and bowerbird mimicry, further examples are also included in the text (see 2.13 and 3.2). These spectrograms are like those used in the inter-observer reliability test. All spectrograms presented use the standard settings available on Avisoft SAS LabLight (version 3.74, R. Specht, 1999: FFT length = 256, frame size = 100%, window = Hamming, overlap between frames = 50%).

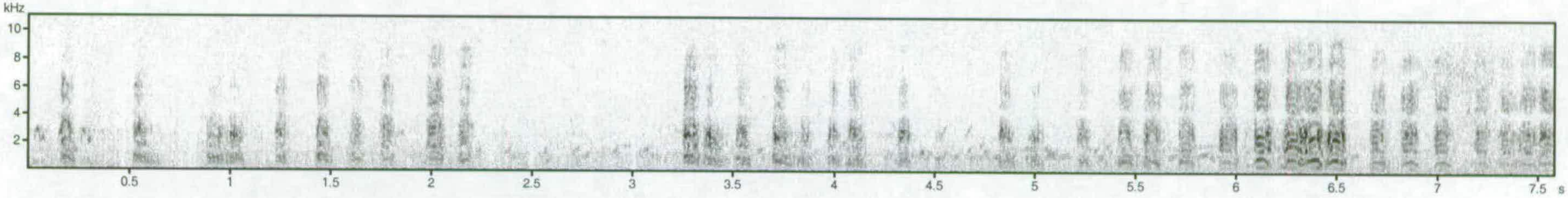

Fig A.1: Grey crowned babbler (*Pomatostomus temporalis*)

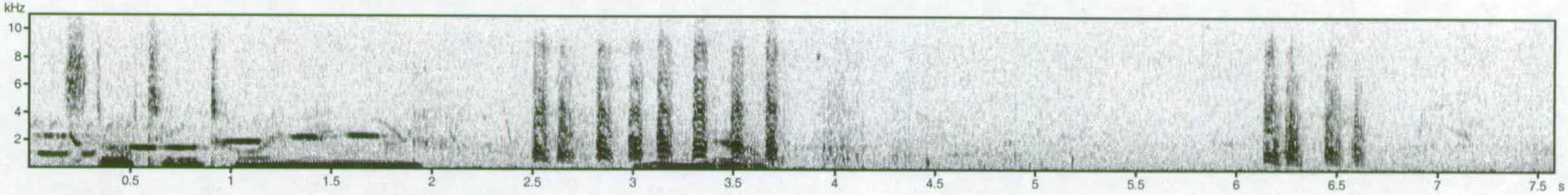

Fig A.2: Bowerbird mimicry of grey crowned babbler

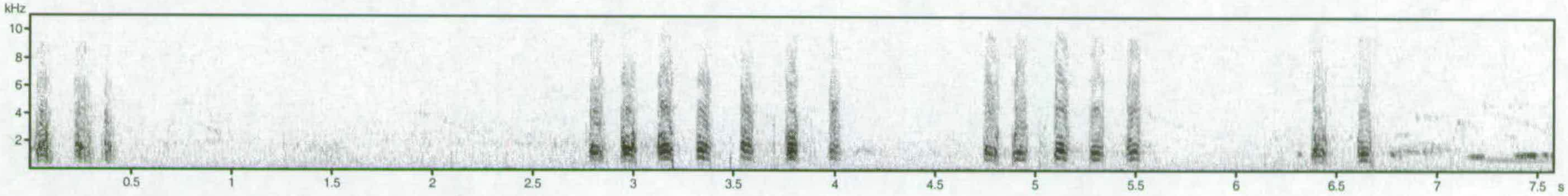

Fig A.3: Bowerbird mimicry of grey crowned babbler

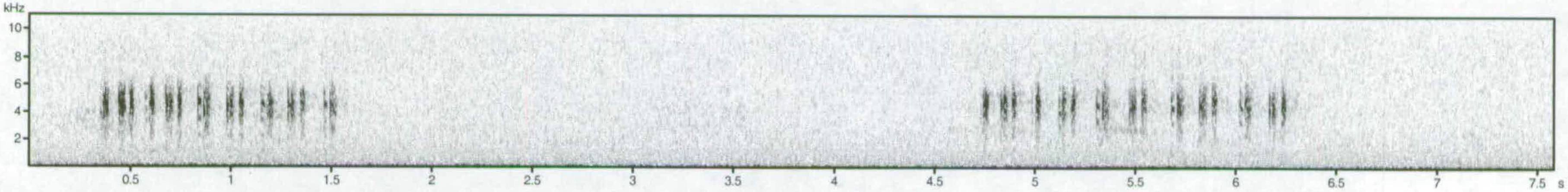

Fig A.4: Willie wagtail (*Rhipidura leucophrys*)

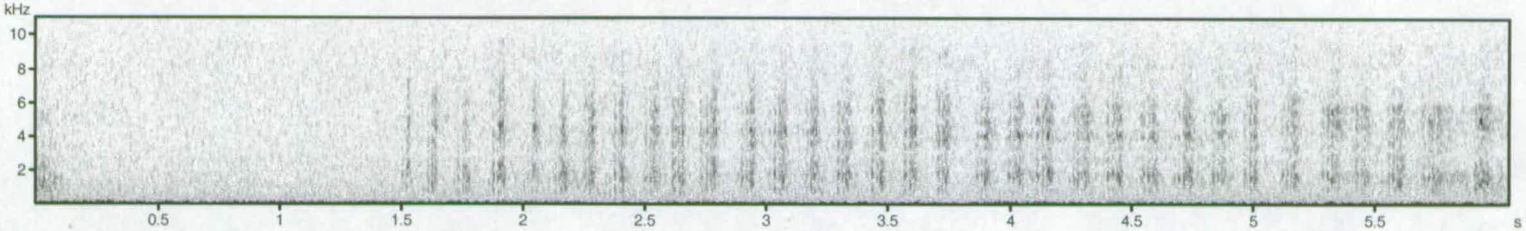

Fig A.5: Bowerbird mimicry of willie wagtail

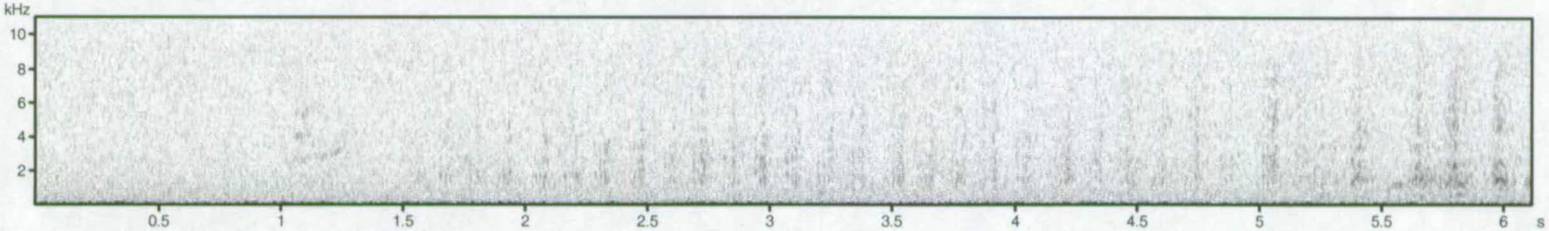

Fig A.6: Bowerbird mimicry of willie wagtail

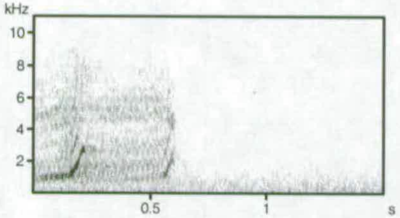

Fig A.7: Pied butcherbird (*Cracticus nigrogularis*) "eerik" call (note only recording not obscured by other calls)

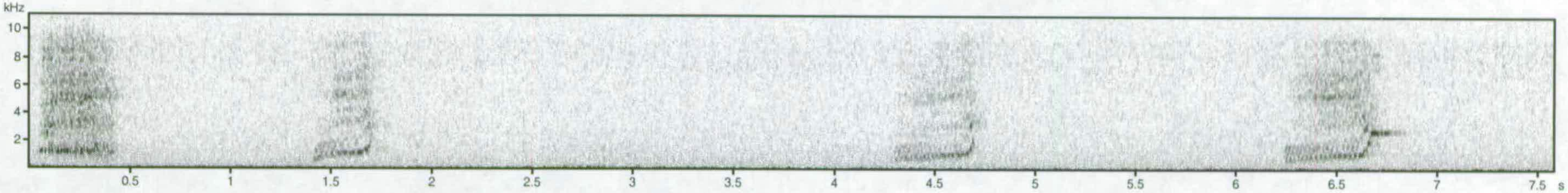

Fig A.8: Bowerbird mimicry of butcherbird (note species-specific hiss at 0 seconds)

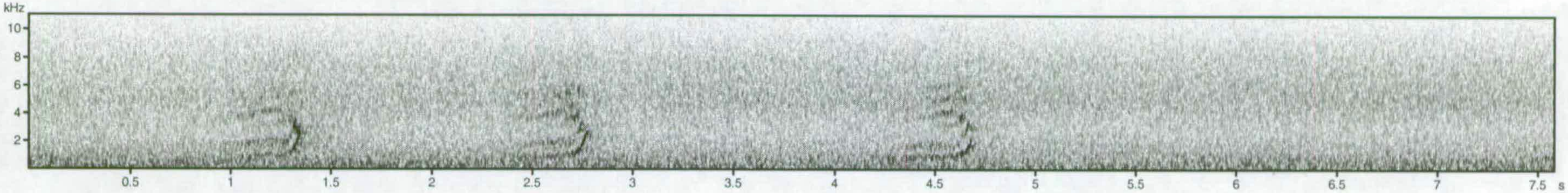

Fig A.9: Bowerbird mimicry of butcherbird

A.2 List of competitive species

1. Conservative assumption (see 3.2)

Non-competitors (all)
Apostle
Babbler
Bee-eater, rainbow
Butcherbird, grey
Butcherbird, pied
Choughs, white winged
Cockatoo, sulphur crest
Crow, Torresian
Dove, bar shouldered
Dove, diamond
Dove, peaceful
Fairy wren, red backed
Fairy wren, variegated
Fantail, grey
Finch, double barred
Friar, little
Friar, noisy
Gerygone, white throated
Honeyeater, blue faced
Honeyeater, brown
Honeyeater, singing
Honeyeater, spiney cheeked
Jacky winter
Kite, whistling
Kookaburra, blue-winged
Kookaburra, laughing
Lorikeet, rainbow
Magpie
Magpie lark
Miner, noisy
Pardalote, striated
Parrot, red-winged
Pipit Richard's
Robin, red-capped
Shrike thrush, grey
Sitella, vaired
Wagtail, willie
Weebill
Whistler, rufous
Woodswallow, black faced

2. Extreme assumption

Non-competitors
Apostle
Babbler
Bee-eater, rainbow
Butcherbird, grey
Butcherbird, pied
Cockatoo, sulphur crest
Crow, Torresian
Dove, bar shouldered
Dove, diamond
Dove, peaceful
Fairy wren, red backed
Fairy wren, variegated
Fantail, grey
Finch, double barred
Friar, little
Friar, noisy
Gerygone, white throated
Honeyeater, blue faced
Honeyeater, brown
Honeyeater, singing
Honeyeater, spiney cheeked
Kite, whistling
Kookaburra, blue-winged
Kookaburra, laughing

Competitors
Magpie
Magpie lark
Miner, noisy
Pardalote, striated
Parrot, red-winged
Pipit Richard's
Robin, red-capped
Shrike thrush, grey
Sitella, vaired
Wagtail, willie
Weebill
Whistler, rufous
Woodswallow, black faced
Lorikeet, rainbow
Choughs, white winged

A.3 List of aggressive species

1. Conservative assumption

Non-aggressive
Babbler
Bee-eater, rainbow
choughs, white winged
Cockatoo, sulphur crest
Dove, bar shouldered
dove, diamond
Dove, peaceful
fairy wren, red backed
fairy wren, variegated
Fantail, grey
Finch, double barred

Aggressive
Apostle
Butcherbird, grey
Butcherbird, pied
Crow, Torresian
Kookaburra, blue-winged
kookaburra, laughing
Magpie
miner, noisy

Friar, little
Friar, noisy
Gerygone, white throated
Honeyeater, blue faced
Honeyeater, brown
honeyeater, singing
honeyeater, spiney cheeked
Jacky winter
Kite, whistling
Lorikeet, rainbow
magpie lark
pardalote, striated
parrot, red-winged
pipit Richard's
Robin, red-capped
Shrike thrush grey
Sitella, vaired
Wagtail, willie
Weebill
Whistler, rufous
Woodswallow, black faced

2. Extreme assumption

Non-aggressive
Bee-eater, rainbow
Cockatoo, sulphur crest
Dove, bar shouldered
dove, diamond
Dove, peaceful
fairy wren, red backed
fairy wren, variegated
Fantail, grey
Finch, double barred
Friar, little
Friar, noisy
Gerygone, white throated
Honeyeater, blue faced
Honeyeater, brown
honeyeater, singing
honeyeater, spiney cheeked
Jacky winter
Lorikeet, rainbow
magpie lark
pardalote, striated
parrot, red-winged
pipit Richard's
Robin, red-capped
Shrike thrush grey

Aggressive
Apostle
Butcherbird, grey
Butcherbird, pied
Crow, Torresian
Kookaburra, blue-winged
kookaburra, laughing
Magpie
miner, noisy
Babbler
Kite, whistling
choughs, white winged

Sitella, vaired
Wagtail, willie
Weebill
Whistler, rufous
Woodswallow, black faced

A.4 List of commonly and rarely heard species

Common
Apostle
Babbler
Butcherbird
Crow
Double bar finch
Fairy wren
Fantail, grey
Finch, other
Friarbird, little
Friarbird, noisy
Gerygone, white throated
Honeyeater, brown
Honeyeater, singing
Honeyeater, spiney cheeked
Magpie
Magpie lark
Miner, noisy
Pardalote, striated
Parrot, red-winged
Rufous whistler
Shrike thrush grey
Sulphur crest cockatoo
Thornbill
Weebills
Willie wagtail

Rare
Bee-eater, rainbow
Bush stone curlew
Cat
Cuckoo shrike, black-faced
Currawong
Dog
Dove, bar shouldered
Dove, peaceful
Dove, other
Duck
Eagle, wedge-tailed
Emu
Falcon, brown
Honeyeater, blue-faced
Jackie winter
Kingfisher, red backed
Kite, whistling,
Kookaburra, blue-winged
Kookaburra, laughing
Lorikeet, rainbow
Pipit, Richard's
Robin, red capped
Rosella, pale-headed
Sitella, varied
White winged choughs
Woodswallow, black-faced

A.5 Presentation experiment

Bower	Presentation 1	Presentation 2	Presentation 3	Presentation 4
3	dove	brown falcon	control	crow
5	crow	control	brown falcon	dove
8	dove	control	brown falcon	crow
9	control	dove	crow	brown falcon
10	control	crow	dove	brown falcon
11	brown falcon	dove	crow	dove
12	brown falcon	dove	dove	crow
13	control	dove	crow	brown falcon
17	brown falcon	crow	dove	control
19	dove	control	brown falcon	crow
21	control	crow	dove	brown falcon
23	dove	brown falcon	control	crow
31	brown falcon	crow	dove	control
32	crow	control	brown falcon	dove

Table A.1: Order of presentation of mounts at 14 bowers (see 4.2). Note data could not be collected from presentations in shaded cells due to (pale grey) absence of bower owner or (dark grey) failure of DAT recorder.

A.6 Playback experiment

Track number	Description
1	species-specific hiss
2	species-specific hiss
3	species-specific hiss
4	butcherbird "eerik"
5	butcherbird "eerik"
6	butcherbird "eerik"
7	babbler
8	babbler
9	babbler
10	brown falcon
11	brown falcon
12	brown falcon
13	display hiss
14	display hiss
15	display hiss
16	white noise
17	white noise
18	white noise

Table A.2: Tracks used during playback (see 4.4)

	Track number		
Bower	**Playback 1**	**Playback 2**	**Playback 3**
2	1	~~5~~	~~9~~
3	6	~~16~~	~~11~~
5	9	14	~~16~~
8	7	12	~~2~~
9	3	16	~~5~~
10	14	~~15~~	~~6~~
11	17	~~5~~	~~7~~
13	10	16	~~13~~
17	6	12	1
18	15	~~11~~	~~7~~
19	1	~~16~~	~~4~~
21	2	~~14~~	~~10~~
23	11	~~12~~	~~7~~
31	18	6	~~1~~
32	14	~~7~~	~~9~~
33	3	~~12~~	~~15~~
35	13	16	~~1~~
36	9	~~1~~	~~10~~
37	4	~~7~~	~~17~~

Table A.3: Proposed playback experiment: playbacks did not occur because (pale grey) bowerbirds were not present or (diagonal line) a decision was made to discontinue the experiment.

A.7 Individual bowerbirds

Bowerbird ID number	Bower number	Status	Minimum tenure in 2002	Minimum tenure 2003	Known tenure?
1	3	owner	5	6	yes
2	9	owner	5	6	yes
3	10	owner	5	6	yes
4	17	owner	5	6	yes
5	2	owner	4	5	yes
6	12	owner	3	4	yes
7	21	owner	3	4	yes
8	23	owner	3	4	yes
9	32	owner	3	4	yes
10	13	owner	n/a	1	yes
11	13	owner	4	5	no
12	31	owner	3	4	no
13	5	owner	1	2	no
14	8	owner	1	2	no
15	11	owner	1	2	no
16	19	owner	1	2	no
17	18	owner	n/a	1	no
18	33	owner	n/a	1	no
19	36	owner	n/a	1	no
20	37	owner	n/a	1	no
21	38	owner	n/a	1	no
22	5	auxiliary	n/a	n/a	n/a
23	11	auxiliary	n/a	n/a	n/a
24	12	auxiliary	n/a	n/a	n/a
25	13	auxiliary	n/a	n/a	n/a
26	21	auxiliary	n/a	n/a	n/a
27	23	auxiliary	n/a	n/a	n/a
28	23	auxiliary	n/a	n/a	n/a
29	31	auxiliary	n/a	n/a	n/a

Table A.4: Identity of individual bowerbirds (see 5.1)

A.8 Inter-bower distances

Bower	3	5	8	9	10	11	12	13	17	19	21	23	31	32
3		3.76	6.16	5.81	10.00	1.74	8.87	7.71	8.70	1.20	4.10	2.10	2.99	3.31
5	3.76		9.80	8.99	12.85	2.28	11.93	10.70	10.48	4.69	7.80	1.84	5.65	6.71
8	6.16	9.80		2.34	9.36	7.89	7.93	7.39	10.72	5.10	2.11	7.98	6.62	5.06
9	5.81	8.99	2.34		11.41	7.49	9.98	9.29	12.20	4.61	2.89	7.17	7.29	6.03
10	10.00	12.85	9.36	11.41		10.68	1.43	2.33	4.21	10.09	8.75	11.85	7.25	6.77
11	1.74	2.28	7.89	7.49	10.68		9.71	8.49	8.68	2.89	5.82	1.38	3.43	4.43
12	8.87	11.93	7.93	9.98	1.43	9.71		1.23	4.57	8.86	7.35	10.81	6.29	5.58
13	7.71	10.70	7.39	9.29	2.33	8.49	1.23		4.00	7.77	6.54	9.61	5.06	4.45
17	8.70	10.48	10.72	12.20	4.21	8.68	4.57	4.00		9.28	9.31	10.03	5.73	6.30
19	1.20	4.69	5.10	4.61	10.09	2.89	8.86	7.77	9.28		3.13	2.89	3.58	3.33
21	4.10	7.80	2.11	2.89	8.75	5.82	7.35	6.54	9.31	3.13		6.02	4.63	3.21
23	2.10	1.84	7.98	7.17	11.85	1.38	10.81	9.61	10.03	2.89	6.02		4.62	5.34
31	2.99	5.65	6.62	7.29	7.25	3.43	6.29	5.06	5.73	3.58	4.63	4.62		1.66
32	3.31	6.71	5.06	6.03	6.77	4.43	5.58	4.45	6.30	3.33	3.21	5.34	1.66	

Table A.5: Inter-bower distances 2002 (km)

Bower	2	3	5	8	9	10	11	13	15	17	18	19	21	23	31	32	36	37	38
2		1.62	5.33	4.51	4.33	9.45	3.36	7.11	8.87	3.04	0.77	2.48	3.57	3.31	2.75	11.41	13.67	9.08	16.74
3	1.62		3.77	6.14	5.80	9.97	1.74	7.67	8.67	2.23	1.16	4.09	2.13	2.99	3.30	13.02	15.23	8.57	18.01
5	5.33	3.77		9.77	8.99	12.81	2.30	10.68	10.47	3.19	4.66	7.81	1.84	5.66	6.72	16.47	18.45	9.72	20.37
8	4.51	6.14	9.77		2.26	9.46	7.87	7.45	10.77	6.98	5.12	2.12	7.95	6.65	5.09	6.98	9.45	11.63	13.57
9	4.33	5.80	8.99	2.26		11.42	7.48	9.27	12.19	5.89	4.64	2.89	7.16	7.30	6.03	7.53	9.49	12.80	12.50
10	9.45	9.97	12.81	9.46	11.42		10.63	2.34	4.14	12.17	10.09	8.75	11.84	7.21	6.75	14.13	17.08	5.90	22.53
11	3.36	1.74	2.30	7.87	7.48	10.63		8.45	8.65	2.64	2.86	5.81	1.41	3.43	4.42	14.76	16.95	8.19	19.52
13	7.11	7.67	10.68	7.45	9.27	2.34	8.45		3.99	9.86	7.76	6.51	9.60	5.03	4.42	12.86	15.76	5.50	20.83
15	8.87	8.67	10.47	10.77	12.19	4.14	8.65	3.99		10.85	9.26	9.29	10.04	5.70	6.28	16.74	19.60	1.76	24.33
17	3.04	2.23	3.19	6.98	5.89	12.17	2.64	9.86	10.85		2.28	5.26	1.52	5.21	5.45	13.42	15.30	10.61	17.25
18	0.77	1.16	4.66	5.12	4.64	10.09	2.86	7.76	9.26	2.28		3.16	2.86	3.59	3.34	11.92	14.09	9.34	16.88
19	2.48	4.09	7.81	2.12	2.89	8.75	5.81	6.51	9.29	5.26	3.16		6.02	4.64	3.20	9.09	11.52	9.94	15.25
21	3.57	2.13	1.84	7.95	7.16	11.84	1.41	9.60	10.04	1.52	2.86	6.02		4.65	5.36	14.63	16.64	9.60	18.76
23	3.31	2.99	5.66	6.65	7.30	7.21	3.43	5.03	5.70	5.21	3.59	4.64	4.65		1.67	13.55	16.11	5.77	19.79
31	2.75	3.30	6.72	5.09	6.03	6.75	4.42	4.42	6.28	5.45	3.34	3.20	5.36	1.67		11.92	14.52	6.77	18.45
32	11.41	13.02	16.47	6.98	7.53	14.13	14.76	12.86	16.74	13.42	11.92	9.09	14.63	13.55	11.92		2.95	17.94	9.13
36	13.67	15.23	18.45	9.45	9.49	17.08	16.95	15.76	19.60	15.30	14.09	11.52	16.64	16.11	14.52	2.95		20.75	6.65
37	9.08	8.57	9.72	11.63	12.80	5.90	8.19	5.50	1.76	10.61	9.34	9.94	9.60	5.77	6.77	17.94	20.75		25.16
38	16.74	18.01	20.37	13.57	12.50	22.53	19.52	20.83	24.33	17.25	16.88	15.25	18.76	19.79	18.45	9.13	6.65	25.16	

Table A.6: Inter-bower distances 2003 (km)