

SONG STRUCTURE AND FUNCTION OF MIMICRY IN THE AUSTRALIAN MAGPIE (*Gymnorhina tibicen*): COMPARED TO THE LYREBIRD (*Menura ssp.*)

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ABSTRACT: This paper compares two species of songbird with the aim of elucidating the function of song and also of mimicry. It attempts to understand why some birds mimic and takes as examples the lyrebird (*Menura sp.*) and the Australian magpie (*Gymnorhina tibicen*). Mimicry by the magpie and its development has been recorded and analysed. The results show that magpies mimic in the wild and they do so mimicking species permanently settled in their own territory. So far 15 types of mimicry have been identified. One handraised Australian magpie even developed the ability to vocalise human language sounds, words and phrases. Results show that mimicry is interspersed into their own song at variable rates, not in fixed sequences as in lyrebirds. In one case it was possible to show an extremely high retention rate of learned material and a high plasticity for learning. Spectrogram comparisons of sequences of mimicry with the calls of the original species, and comparison of magpie mimicry with lyrebird mimicry is made. Both species may justifiably vie for the position of the foremost songbirds of Australia, and both are territorial, yet the function, structure and development of song are different in the two species. It is argued that possible functions of mimicry are related not only to social organisation but also to the niche each species occupies. Territoriality may go some way to explaining the complexity of song but not necessarily the different functions of mimicry or the varying degrees of complexity of communication. We need to ask what conditions may foster development of complex communication patterns in avian species.

INTRODUCTION

Two of the foremost songbirds of Australia, and possibly the world, are the Australian magpie (*Gymnorhina ssp.*) and the lyrebird (*Menura ssp.*). Both are also the most prolific Australian mimics in the wild. Until recently, knowledge of mimicry by magpies in the wild was confined to popular knowledge and speculation. Here it is shown that

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the Australian magpie is capable of very complex vocal communication, including carolling and mimicry (Kaplan, 1998). The lyrebird, especially the superb lyrebird (*Menura novaehollandiae*), has one of the most powerful songs of any bird and it is widely known for its spectacular mimicry (Robinson & Curtis, 1996). The purpose of comparing two ancient Australian songbird species is to propose that song structure, including mimicry, may appear to be similar in each species but serve different functions.

Until now it was not possible to compare the song structure of lyrebirds with magpies because too little was known about the mimicry of magpies, or of any other Australian bird using mimicry. Although the magpie has been comparatively well researched in relation to other Australian songbirds, it is still surprising how little systematic work has appeared on the song of the magpie. There exists just one major study of vocalisation in magpies, published in three parts (Brown & Farabaugh, 1991; Brown, Farabaugh & Veltman, 1988; Farabaugh, Brown & Veltman, 1988). Many of the earlier vocalisation data by Robert Carrick and colleagues were never published (Carrick, 1963; Carrick, 1972). This paper reports the incorporation and retention of mimicked sequences, including the human voice, in magpies and lyrebirds. The data of magpies is based on the author's own research, whereas the examples of lyrebird mimicry are drawn from other researchers for comparison only.

Mimicry is not a rare occurrence amongst avian species. In 1934 Chisholm identified 56 Australian avian species with some skills in mimicry (Chisholm, 1948) and since then about half of those identified have been verified by ornithologists. While some forms of mimicry might be impossible due to anatomical limitations (Thorpe, 1961), mimicry appears to be a ubiquitous avian phenomenon. In the 1970s Gramza even postulated that eventually most species of birds will be found to have some ability to copy extra-specific sounds (Gramza, 1972).

The Australian magpie and the lyrebird lend themselves to comparison. Both have an ancient lineage amongst the Australo-Papuan centred corvida (Schodde & Mason, 1999; Sibley & Ahlquist, 1985). Both are territorial and ground feeders and both are capable of producing loud and musical notes that are widely audible. Their frequency range is similar and their skills in and extent of using mimicry are similar, as this paper shows, although the lyrebird, with its three syringeal muscles, rather than the oscines' typical four, is possibly more flexible.

However, the social organisation and the breeding and dispersal strategies of the lyrebird and the magpie differ from one another. The

Australian magpie is an exemplary model for several reasons. Although the female builds the nest alone and incubates the eggs by herself, males and females share in raising the young (Queensland National Parks, 1987). Males may also feed the female during the weeks of incubation. Australian magpies, in common with many other members of the corvidae family (white-winged choughs, apostlebirds, crows, currawongs), have very complex social relationships, reflected in complex vocal communication and, at times, cooperative breeding or hunting (Cockburn, 1996; Farabaugh, Brown & Hughes, 1992; Veltman, 1984). Territoriality, cooperative breeding and hunting (O'Neill & Taylor, 1984) are signs of complex social organisation. These criteria have favoured the development of complex song and communication patterns in both sexes (Brown & Farabaugh, 1991; Brown *et al.*, 1988).

Song, in Australian magpies, is not used specifically for courtship (Brown and Veltman, 1987) and, therefore, sexual competition has not led to a male developing a song that is more elaborate than that of another male, nor does singing bestow an advantage to the male alone (Kaplan, 1998). Moreover, not only do both males and females sing throughout the year, but also duetting occurs between males and females (Brown *et al.*, 1988; Farabaugh, 1982). Male and female singing is, however, not confined to pair duetting or territorial defence. Duetting between males and females is thought to have evolved in dense tropical rain forest habitats, as a means of staying in touch when visual contact may be difficult (Catchpole & Slater, 1995). Such a conclusion cannot be drawn for the Australian magpie, since they are very widespread in open areas and occur across the Australian continent, with the exception for areas of desert (Carrick, 1972). Hence, the species occurs in a wide variety of climate zones. Indigenous to Australia, but also introduced to New Zealand (McIlroy, 1968) and some islands of Fiji (Clunie & Morse, 1984), Australian magpies have adapted to tropical and subtropical regions and they are particularly widespread in temperate zones (Baker, Mather & Hughes, 1995; Burton & Martin, 1976).

By contrast, lyrebirds occupy only a relatively small stretch of the east coast of Australia and live in areas of remaining dry sclerophyll and wet forests. Rainforest (whether temperate or subtropical) is its main habitat. There are two species, the superb lyrebird (*Menura novaehollandiae*) with a wide but patchy distribution extending from near Melbourne to the rainforest hinterland of Brisbane. The Albert lyrebird (*Menura alberti*) is now found only in very small patches of rainforest southwest of Brisbane, at the northern border of New South Wales. Males are polygamous and promiscuous and they fertilise

several females in a season (Schodde & Mason, 1999). They take no share in nestbuilding, incubation or in rearing the young but it appears that the young males later take their father as tutor for song-learning. Lyrebirds are scrub-birds and are vulnerable to predation whereas magpies are not. Magpie young disperse far from the parent territory, whereas lyrebird offspring stay close by. Powy's seven-year study found that amongst the superb lyrebird groups studied (seven in all), there was structural, locational and temporal constancy of territorial song from one generation to the next (Powys, 1995). There were also distinct regional dialects which were maintained over generations.

Magpie song has been found to fall into several distinct categories. One category includes the pre-dawn/nocturnal calls. They are relatively stereotyped monotonous songs in the summer months, or, as Sanderson and Crouche argued, during the breeding season only. Another category is the territorial song containing loud individual calls and carolling of two or more magpies. A third is the subsong, an individual song (Sanderson & Crouche, 1993). Mimicry is found only within this third category. There are also a variety of context specific calls (see also Robinson, 1956; Robinson, 1975) that could, conceivably form a fourth category. In lyrebirds, one can distinguish mainly two forms of song: the territorial song and the breeding song. The territorial song may contain percussion sounds and it is shown in this paper that it usually has a relatively simple structure. The breeding song, however, is complex and mimicry is found in the breeding song only (Robinson & Curtis, 1996). There is some suggestion that lyrebirds do not use all their mimicked sounds in the breeding song but only those that are loud and clear (Readers Digest, 1976) but no research has proven or disproven this statement to date.

This paper reports evidence of incorporation of mimicry into magpie song from different regions in Australia for the two subspecies, the black-backed magpie of eastern Australia (*G. tibicen*) and the white-backed magpie of southern and western Australia (*G. hypoleuca*).

METHODS

The study used the vocalisations of 22 magpies, including only those that produced mimicked sounds. Two of them were handraised magpies. These were not the only magpies raised. Of the eighteen magpies that were hand-raised between 1995 and 2000, only two developed mimicry and one of them (Bird A), held in the territory for one year, developed extensive skills in mimicry. For those two mimicking magpies, an aviary was placed near the house and the

observer was unseen by the magpies. A standard unidirectional microphone was attached to a stand at a height of 1.80 m, situated 20 cm from the main perching branch of each individual bird. The observer was unseen and a Sony field cassette recorder was operated from inside the house at any time when vocalisations occurred. Vocal development of Bird A was recorded for a period of half a year, with observation times of 12 hours per day for six days a week, dropping to 10 hours per day and 5 days a week after half a year. This study concluded after 12 months and the bird was successfully released. The vocalisations of the other hand-raised mimicking bird (Bird B) were recorded for a period of three months only because it was ready for release after three months of care. Australian magpies, as all native Australian fauna, are a protected species and handraising them can occur only under licence and for the purpose of release. Birds cannot be held beyond the time needed for total recovery. The birds were cared for under licence and the research conformed to the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (1997).

Both birds, in separate aviaries and in different years (Bird A from late 1995 to late 1996 and Bird B from late September 1997 to early December 1997) were held in aviaries under cover but they had ample sunlight each day and access to water and food *ad libitum*. Initially, both had to be hand-fed at half hour intervals from 6am to 7pm each day. In the case of Bird A, handfeeding was for a duration of two months, and in the case of Bird B for one month. Both birds were found within the broad geographical area of the New England Tableland, a temperate climate zone, 1200 m above sea level in north west New South Wales, and they were reared on a property near Armidale.

An extra 20 magpies were part of this study and they were wild magpies and the data were obtained from field sound recordings. The method for obtaining these data had to be unconventional. Mimicry by magpies in the wild is too sporadic for systematic study and is not always witnessed unless accidentally overheard in the field or occurring near human dwellings. To achieve a wider sample than had been secured in captivity, I was given permission during an interview on the ABC Science Show radio program (on air 28 December 1996) to ask listeners to send in tapes and detailed accounts of whether they had ever heard a magpie mimic. The response was overwhelming. Over the next three months well over 100 letters and telephone calls were received. Only a few respondents had actually recorded the mimicry but these respondents were willing to send their taped information. Some information was not useable due to the quality of the tapes but

nine tapes were suitable for analysis, yielding separate recordings of mimicry (N=9).

These specific mimicked vocalisations by magpies derived from different territories, and hence were assumed to be of unrelated individuals and non-overlapping territories. Recordings used for analysis came from Western Australia (N=1), South Australia (N=1), Victoria (N=3, different townships), New South Wales (N=2, different townships), the Australian Capital Territory (N=1) and Queensland (N=1). Respondents of useable tapes were additionally asked whether they knew the sex and age of the taped individuals and whether any individuals had been hand-raised, were tamed or wild. They were also asked if they knew whether the mimicked species were permanent residents in the magpies' territory. Not one of the recorded birds had been hand-raised and only one was tame enough to take some food supplied by humans. All others were wild and had been in their respective territories for some years. Not all respondents were clear of the sex of the bird they had recorded. In magpies, morphological sex differences are minimal and may, at times, be difficult to identify. It was certain, however, that not one of the recorded birds was a juvenile. Juveniles have different plumage to adults and are therefore easily identified. In every case, the mimicked sounds derived from permanent residents.

In addition, I was able to peruse some of the tapes derived from a study of magpie vocalisations undertaken by John Carrick, Norman Robinson and Bruce Falls in the Canberra area in 1965. These had never been used for publication. The tapes were generously provided by Prof. Bruce Falls (Canada) and they were annotated so that it was possible to establish age and sex and context of the mimics. Thus the total number of analysed mimics derived from other sources came to ten, and the complete sample size was N= 12, including the hand-raised magpies. This is the largest sample of mimicry recordings of magpies.

Mimicry and its development was examined and analysed using the sound analysis program 'Canary', developed by Cornell University. Initially, Canary 1.2 was used and, with a later system, this was changed to Canary 1.2.4, without loss of data to the original recordings. This analysis yielded sound spectrograms and waveforms.

Wherever possible, the mimicked species were recorded separately. This was possible in all cases of the mimicry displayed by the hand-raised magpies, but substitutes had to be found for almost all sounds submitted from around Australia. Spectrogram comparisons of mimicked sequences with the original species and with lyrebird mimicry were made. The lyrebird recordings were those of commercially available recordings from 'Birds Australia'.

The tapes were analysed to find mimicry. It became clear on listening to tapes supposed to contain mimicry that a definition of mimicked sounds was needed. By definition, a bird could not produce mimicry of sounds that fell outside its own physiological vocal range. Just because a vocalisation sounded 'different', it might not necessarily be regarded as mimicry.

The definition of mimicry that was ultimately adopted was derived not just from auditory sampling but from assessing visual images of the sounds in question. Copying was disregarded as mimicry if it occurred only once. 'False' mimicry was classified as brief moments of odd sound modulations that suggested other influences but were not structured sufficiently to be included. There were often suggestions of mimicry which were discarded because they fell into the typical sound structure range of magpies. These were therefore regarded as variations on the species-specific song.

Vocalisations accepted as 'true' mimicry had to fulfill four specific conditions: a sample presented a special pattern of sound that was atypical of the normal structure of magpie song. Second, the pattern had to be repeated and occur again in the song repertoire. Third, in repeating the same structure, a break with its typical species-specific call had to occur and, fourthly, the atypical sound pattern needed to be identifiable as a species-specific pattern of the vocalisations of another species. Only those vocalisations that fulfilled all four variables were then subjected to closer analysis. Identification of sounds involved naming the mimicked species. These were isolated and then also sent to the CSIRO Sound Library in Canberra for separate verification.

RESULTS

From the tapes 15 distinct and easily recognisable types of mimicry were identified. Mammal calls included: horse neighing, dog barking, cat meowing, and human voices. The identification of mimicry of other birds was at times more difficult because recognition required knowledge of the vocal repertoire of a wide range of avian species and because sometimes brief sequences of unusual sounds were not unambiguously those of another species. It is possible that some were missed. The mimicked avian species that were identified in wild magpie vocalisations without any element of doubt were: lapwing, lyrebird, kookaburra, currawong, crimson rosella, eastern rosella, red wattlebird, barking owl, and the boobook owl. Figure 1 gives examples of widely different sound structures of mimicry, one of horse neighing and the other of a boobook owl. Note that the sound of the boobook

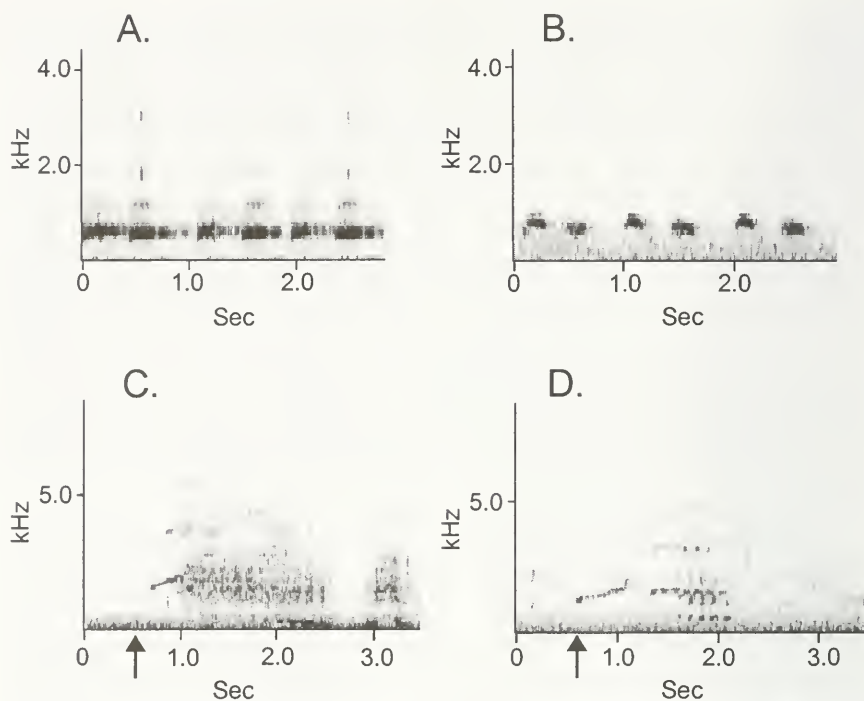


Figure 1. Sonograms of sounds and their mimicry by wild magpies. A, Boobook owl; B, Mimicry of boobook owl. A and B were recorded in northwest New South Wales, Australia; C, Horse neighing; D, Mimicry of horse neighing recorded in Ararat, a town in Victoria, Australia. Arrows in C and D indicate the spikes of sound at the start of the neighing.

owl (not a songbird) is characterised by heavy hooting, largely consisting of noise (hence the broad line). The magpie mimicked this owl very adequately by attempting to stay in the same frequency range (under 1 kHz) and broadly copying the noise. There are no overtones in this rendering. By contrast, the mimicry of the horse neighing is rich in overtones. While it is more musical (clear formants rather than the fuzzy noise of the horse), the magpie has rather faithfully reproduced the structure of the sound. Captive birds also mimicked budgerigars and peachface parrots.

The hand-raised magpies (Birds A and B) yielded 70 hours of vocalisations. Table 1 shows an analysis of species calls that were mimicked by these magpies. (Note that Table 1 excludes all resident small avian species with calls above the frequency range of magpies such as pardalotes, European gold finches, superb blue wrens, silver eyes, several species of robin, eastern spinebills, grey fantails, whitebrowed scrub wren, weebill, house sparrows, white-throated

Table 1. Vocalising species on the property in which Bird A was reared and maintained for 1 year. Note that this bird mimicked only those species that were in close proximity to its own aviary and that were permanent residents on the property. The species listed excludes all resident small avian species with calls above the frequency range of magpies. P, permanent; VR, visitor - regular; VS, visitor - seasonal or seldom.

| Source of Sound | Vocalising species on territory | Mimicked | Status of vocalising species |
|-------------------------------------------|---------------------------------|----------|------------------------------|
| Near Sounds (heard and seen) | Kookaburra | ✓ | P |
| | Peachface parrots | ✓ | P |
| | Budgerigars | ✓ | P |
| | Magpies | ✓ | P |
| | Dogs | ✓ | P |
| | Human voices | ✓ | P |
| | Crimson Rosella | - | VR |
| | Eastern Rosella | - | VR |
| | Galahs | - | VR |
| | Red wattlebirds | - | VR |
| | Grey butcherbird | - | VS |
| | Currawongs | - | VS |
| | Magpie larks | - | VS |
| Distant sounds (heard but not seen) | Car horns | - | |
| | Engine sounds | - | |
| | Lapwings | - | |
| | Donkeys | - | |

gerygone, southern whiteface, and other species that either rarely vocalise or were very rarely seen such as the sacred kingfisher, goshawk, kestrel, crested pigeon, white-backed swallows, feral pigeons, red-rumped parrots and dollarbirds). The analysis of mimicked species showed that not all sounds were copied but only those of significant fauna that permanently shared the same territory as the magpie. These included other captive birds housed near the magpies and household pets, human carers but not any wild species that visited the vicinity of the cages (Table 1).

Certain mimicked sounds were used by Bird A at a higher rate than others. In descending order, the greatest percentage of mimicked calls over a year and calculated as a proportion of all vocalisations were human (mean of 4%), then kookaburra (mean of 3.2%), then peach face (mean of 3%) and, rarely, budgerigars (0.5%). Over a three month period, vocalisations consisted to 70% of species-specific vocalisations whilst the remaining 30% were mimicked items. The practice of mimicked human sounds accounted for a third (11% of total vocalisations), 3% for peachface parrots and 2% for kookaburras. Bird A also used segments of mimicked calls to make new sequences and to

integrate fragments of any mimicked calls into its own song. Dog barking was also found but significantly lower than that of these avian species caged nearby. There were also variations in the amount of mimicry practice in response to hearing specific sounds for the first time. As Figure 2 shows, specific mimic segments received higher or lower amounts of practice when the stimulus changed (Fig. 2A) or was removed (Fig. 2B).

In Figure 2A it can be seen that practice of kookaburra mimicry increased from near zero to over 3% in the month thereafter; in fact, two days after Bird A had been introduced into the adjoining cage. This level was maintained throughout the following month but declined during the two subsequent months. The first kookaburra call lasted less than a minute, yet two days later the magpie gave a complete rendering of that call (see also Fig. 3). Mimicry practice declined in the absence of any further calls. Then a second kookaburra joined the first, as silent as the first, and mimicry practice of the kookaburra sounds declined almost to zero. A month later, the two kookaburras joined for the first time for a duet. After this event, mimicry incorporation of kookaburra sounds increased steeply and remained high for several months thereafter. Interestingly, the practice after the first duet differed from the first mimicry in that the magpie attempted to copy the duet rather

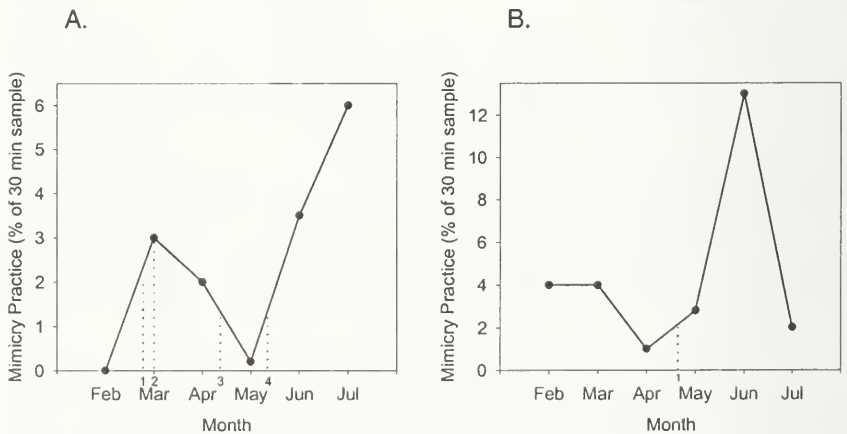


Figure 2. Practice of mimicry by a magpie (referred to as bird A in text) of kookaburra and peachface parrots calls. Data are plotted as the percentage of time spent engaged in mimicry during a sample of 30 mins of all song vocalisations. A. Effect of additional Kookaburra calls on mimicry practice. The additions are shown with dotted lines: 1, First kookaburra call heard for the first time; 2, first instance of mimicry (two days later); 3, second kookaburra arrives; and 4, first duet between the two kookaburras occurs. B. Effect of removal of Peachface parrots calls on mimicry practice. 1, time at which peachface parrots were removed from the outside aviary.

than the individual bird. Mimicry practice of the duetting rose to 6% two months later (Fig. 2A).

It seems significant that the practice of peachface parrot mimicry increased after the birds had been removed (Fig. 2B). Peachface parrots vocalise extensively and their removal to warmer winter quarters, along with the budgerigars, turned the aviary section into a relatively silent area. Instead of decreasing practice of the peachface parrots, Bird A in fact tripled the practice of their mimicry each day for almost an entire month, after which practice of peachface parrot mimicry declined to its earlier low level.

Figure 3 shows sound spectrograms of calls by kookaburras and their mimicry by a lyrebird and a magpie. Note that the magpie has attempted to copy the noise (blurred lines) in its rendering as well as the overtones of the sound rather faithfully: there are seven or eight harmonics in one sound (parallel lines) and the magpie's sound has the same number. Finally, the harmonics are not flat but curved downwards at each end and the magpie has copied this feature exactly. Note by comparison that the lyrebird's rendering is more rapid (8 syllables per 600 ms) than either that of the kookaburra or the magpie's copy. Lyrebirds, with their three syringeal muscles are more flexible. In the lyrebird's mimicry the structure of each harmonic is different, more like an open triangle (see arrow 4 in Fig. 3C) and the rendition is also not as loud as that of the original. Yet to the human ear, this lyrebird's mimicry of kookaburra call sounds very authentic.

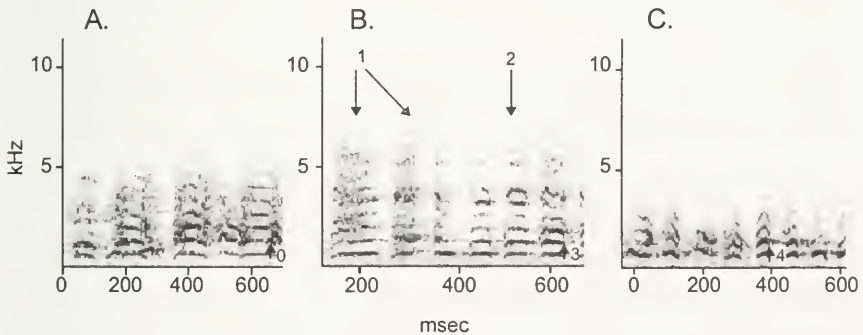


Figure 3. Comparison of mimicry by a magpie and a lyrebird. A, Sound spectrograms of a kookaburra call. B, Mimicry of the kookaburra by a magpie. C, Mimicry of the kookaburra by a lyrebird. Specific features of the call are shown by the arrows: Arrow 1, the magpie copies the noise in its rendering and Arrow 2, overtones of the sound. Arrow 0, the harmonics curve downwards at each end. Arrow 3, faithful copying of this feature by the magpie. Arrow 4, example of lyrebird harmonic.

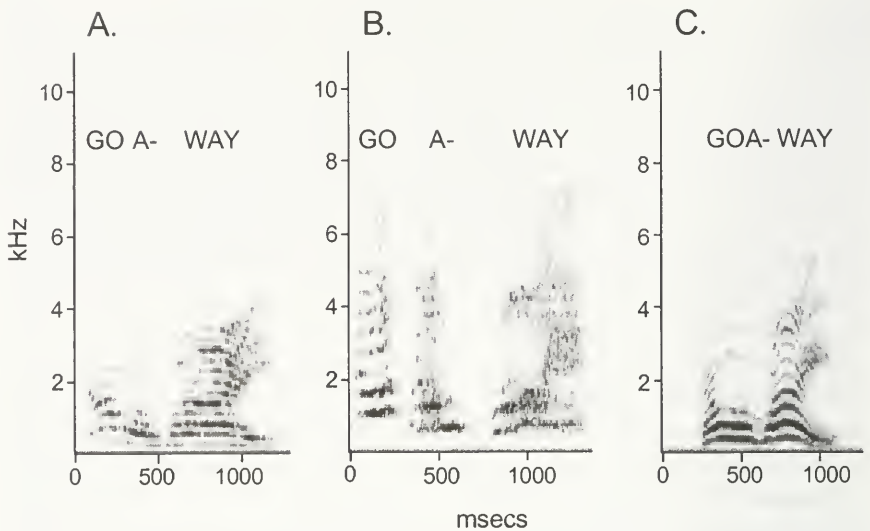


Figure 4. Mimicry of the human voice by a magpie. A. and C. Sonograms of two humans saying 'Go Away". B. Centre panel shows magpie mimicking this phrase.

Both lyrebirds and magpies have been known to mimic human speech. In Figure 4, an example is presented of a human speech segment that Bird A had learned and might have learned from either one or the other of the human voices presented in the sonograms of Figure 4. The human voice has many overtones (indicated by the layers of bars for each sound) and there are substantial variations from one human voice to another (Fig. 4A, C). The magpie gave an audibly recognisable version of the phrase and attempted to use the complex overtone structure of each sound (see especially the syllable "go"). The phrase 'go away' was also clearly understood by people who had never heard a magpie speak. The magpie separated the 'a' from 'away' much more strongly than the human tutors. It is likely that this has to do with the bird's inability to use lips to form some consonants.

It is important to emphasise that the lyrebird's own territorial song is quite simple and substantially different from the sound structures of the calls that lyrebirds and magpies attempt to mimic (Fig. 5). The lyrebird's territorial calls usually have just one formant and few overtones. The magpie's own warble (quiet) song usually consists of a range of complex modulations but with just one formant and few overtones. The results have shown that in mimicry magpies copied rhythm, including pauses, overtones and modulations within each sound in such a way as to create the illusion of some other species vocalisation.

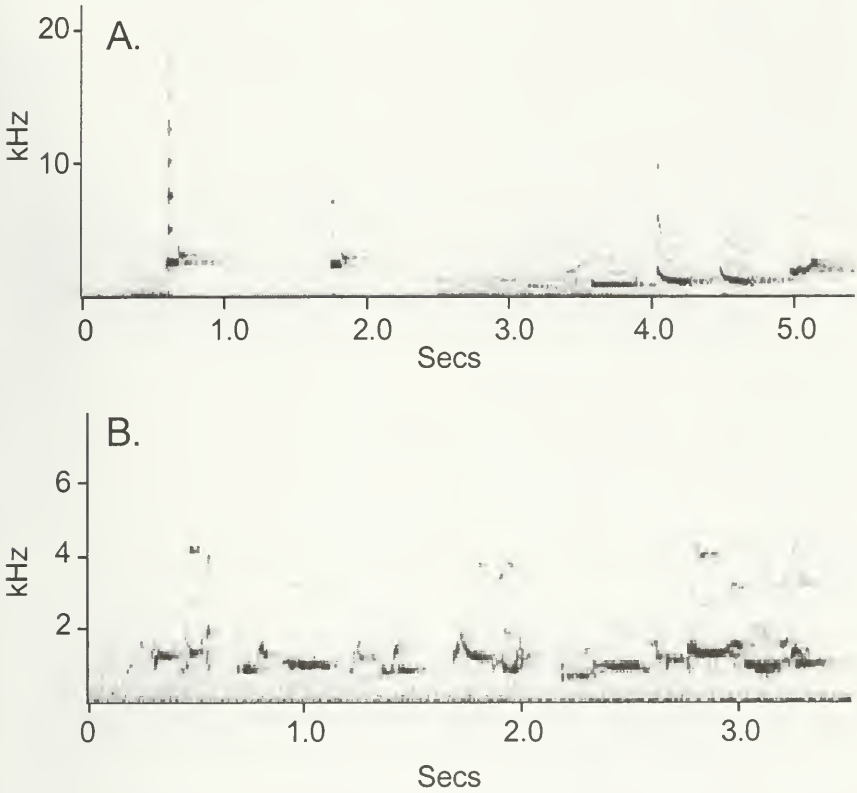


Figure 5. Sonograms of the species-specific song patterns of the A. superb lyrebird (territorial song) and B. the magpie (quiet warble). Pauses are rendered in true time.

The preciseness in the magpie's mimicry of other species was also demonstrated in a variation of mimicry of kookaburras by the magpie. Figure 6 shows the attempt by a magpie to copy not just the sounds of one kookaburra vocalisation but of the specific duets. Here we see that the magpie has accurately copied the two major formants, the flow of continuous sound and the pauses caused by one kookaburra briefly dropping out of the duet.

The study of examples of mimicry by wild magpies found evidence of mimicry of potential predators of young magpies (Fig. 1). One of them is the boobook owl (*Ninox novaeseelandiae*), an owl that is found throughout Australia. As this is only one isolated case, it is not clear whether this result is only a chance result or suggests a significant finding. Boobook owls are nocturnal and, on moonlit nights, magpies are crepuscular and even sing at times during the night. Hence there is opportunity for learning their call and for using it at a time when the

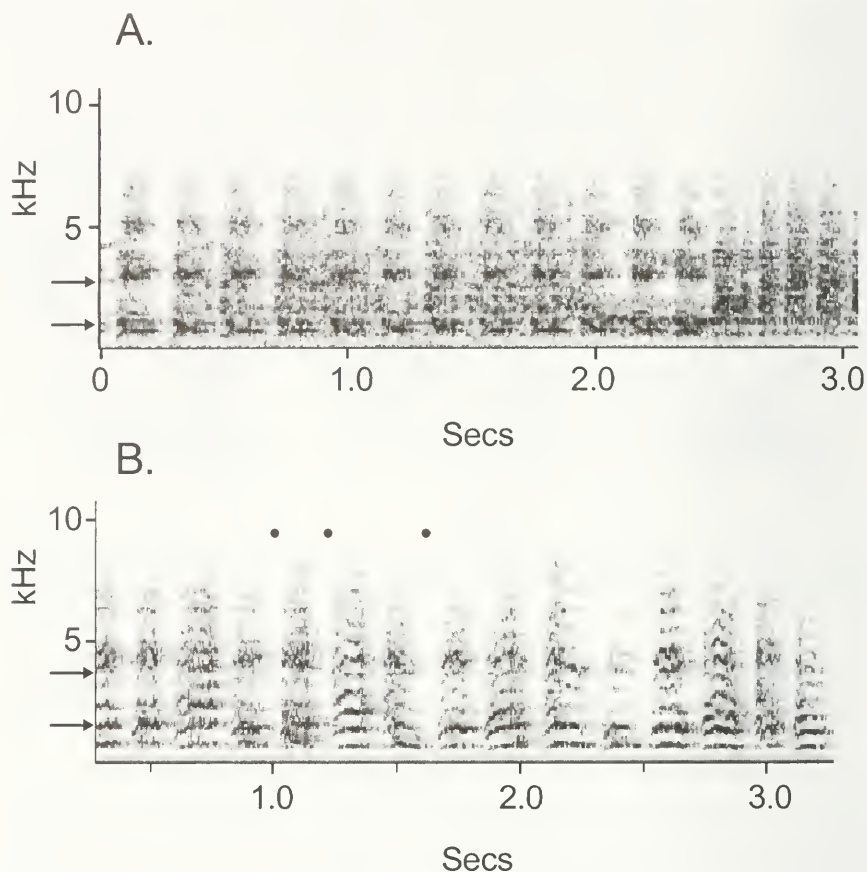


Figure 6. Mimicry of a kookaburra duet by a magpie. A. Sonograms of two captive kookaburras duetting. Only one bird was singing in the broad grey columns 1-3 and 10-12. B. Magpie mimicking the duet. The arrows indicate that the magpie has copied the two formants rather precisely. The dots above the columns show where it has also attempted to mimic the flow of continuous sound with lots of noise. The magpie also attempted to mimic the pauses caused by one kookaburra briefly dropping out of the duet.

owls are active. One isolated case of the mimicry of a barking owl (*Ninox connivens*) was also found amongst examples collected of wild magpies. This example was submitted to me as an example of mimicry of a dog barking. Analysis showed that it was not a dog but the owl. There may be more examples of barking owl mimics that have so far been held to be dog barks. The sounds are easily confused but the sonogram reveals that the structure of a dog bark and the vocalisations of a barking owl are markedly different. The barking owl is a known threat to magpie young.

The study found that magpie mimicry is particularly accurate in

terms of the structure of the sounds that the bird mimics. Figures 1, 3, 4 and 6 show this astuteness very clearly. In particular, it is worth noting the differences of sound structure between those of an owl and a horse (Fig.1) and to assess Figure 3 again, showing the comparison of sound rendition between a real kookaburra, a magpie and a lyrebird. In terms of structure of sounds, the magpie's mimicry is far more accurate than that of the lyrebird. In other words, the lyrebird's mimicry is impressionistic while the magpie's is realistic. It is also important that the same captive bird that learned to mimic the captive kookaburra in close proximity also altered its mimicry of the kookaburra sounds once it had heard the duet of two kookaburras (Fig. 6). The same attention to details of sound structure are evident throughout all examples of mimicry that were collected of wild and captive magpies. The obvious degree of accuracy in rendering the main features of the structure of sound in the mimicry by magpies and the adaptation of that mimicry to new variations are the main findings of this study.

The vocal and auditory achievement of mimicking sounds becomes clear when these are compared to the species-specific vocalisations of either species, magpie and lyrebird. It is important to note that the structure of the lyrebird's song is relatively simple (see Fig. 5) and both species usually remain within a limited frequency range and a limited number of overtones. Both species show pure tones (single dark line) and melodious flow of song. The magpie song is generally more complex. Most vocalisations occur between 400 Hz and 6 kHz.

The results showed that mimicked sequences were incorporated (Fig. 7) in such a way that these incorporations, to some extent, seemed rule governed. Certain basic structures were found in all magpie samples of mimicry collected. For instance, there was not one single example of song closure on a mimicked sound. The bird always returned to one or two of its favourite closing phrases (species-specific) before closure. All mimicked sequences were embedded in one ongoing phrase that ended in closure either of its own individual identification phrase or in a specific three-tone trill (Fig. 7). As can be seen in the lower panel of Figure 7, the individual 'signature' is no more than two to three seconds long. Finally, phrases involving elements of mimicry in magpie song were highly variable. Figure 7 shows the incredible vocal versatility of the magpie's vocal abilities, ranging over four octaves and varying between soft segments, crescendos and strong finales. Note the rapid staccatos of the peachface parrot mimicry.

Unlike lyrebird breeding songs that are characterised by fixed patterns of sequence, the positioning and use of mimicry in magpie song appears to be arbitrary. Establishing the exact sequencing statistically is still a work in progress. There was no apparent regularity

in sequence of mimicked sounds. They seemed to be in random order. By contrast, lyrebirds appear to string mimicked sequences together in an unchanged order, referred to as the Albert cycle (Robinson & Curtis, 1996). Any additions are added on but then the bird eventually returns to the beginning of the sequence and starts all over again in the same order.

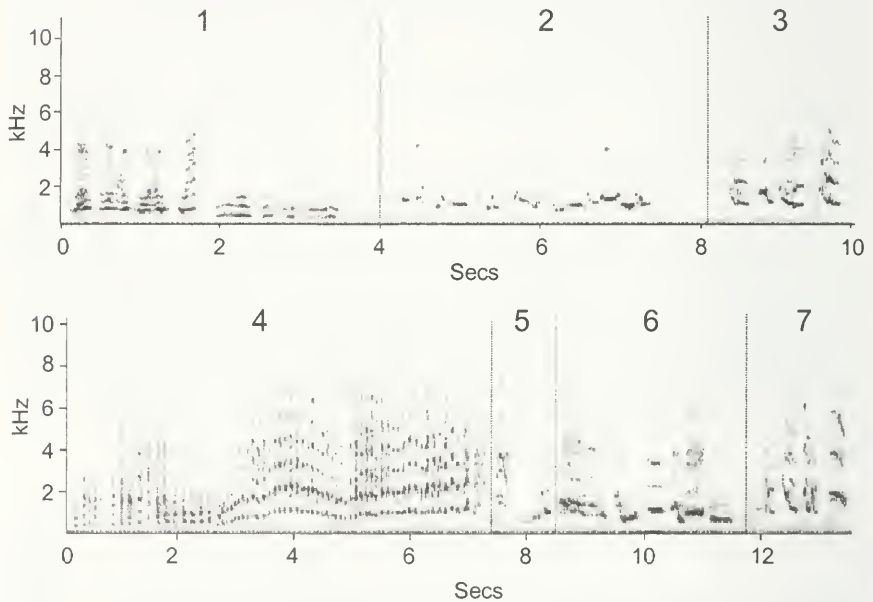


Figure 7. Integration of mimicry into the magpie's own song. The phrases are separated by dotted lines and are marked 1-7. They represent: 1, mimicry of human vowel sounds; 2, species-specific warble (typical song type of magpies); 3, closure of phrase by a four syllable magpie specific call type. Segments 4-7 represent another song; 4, shows the rapid staccato mimicry of peachface parrots; 5, a transition two-syllable call that, in structure, is similar in amplitude and overtones and is a modified magpie alarm call; 6, is a call specific to this individual bird (an individual signature) and 7, indicates closure of the phrase. Note that in this second example, again, the phrase begins with a mimicked sequence, and it ends with a magpie-specific closing phrase (only two or three types of closing phrases were ever used by this individual bird and they never occurred elsewhere in the song).

DISCUSSION

The study is the first to establish that mimicry amongst Australian magpies is not confined to a specific region or subspecies. It occurs in magpies distributed widely across the Australian continent. Furthermore, the results reported here have shown that magpies do not mimic as an artifact of captivity, as many Australian parrot species appear to do, but mimicry patterns freely developed in wild birds. In fact, mimicry is widespread and highly developed amongst Australian bird species in general. The best known species for mimicry in the wild are lyrebirds (both species), Australian magpies and bowerbirds (several species). In contact with humans, even if remaining free, these species can also mimic human speech. Amongst European birds, the starling is the star of mimics (West & King, 1990; West, Stroud & King, 1983). In North America it is perhaps the northern mocking bird. We know that parrots and budgerigars are excellent mimics in captivity but the first examples of parrot mimicry in the wild have been found only recently and for one species only, the Grey parrot (Cruikshank, Gautier & Chappuis, 1993).

My research suggests that, in magpies, mimicry is performed both in solitude and in company, is independent of the breeding season and is voiced by males and females alike. By contrast, the mimicry of the lyrebird is confined to the breeding season and to the breeding song of the male only (Robinson & Curtis, 1996).

The data indicate adaptation and a substantial learning plasticity early in life. The mimicked sounds were not all learned at the same time but at different times throughout the observation period. David Attenborough claimed in his series 'The Life of Birds' (BBC, 1998, Episode 7) that the lyrebirds knew about 20 mimicked sounds. I have found no reference to substantiate this claim. However, if this is true, then the magpie and lyrebird may be very similar in mimicry repertoire size. The present study identified 15 types of mimicry of unambiguous sounds and there might have been more since rigid criteria had to be met before a sequence was considered to be mimicry.

Sampling of mimicry in lyrebirds in the wild is relatively accessible because the breeding song is part of a breeding display. The male clears a mound within the forest and dances. Time and place for the vocal performance are fixed and the amplitude of the song, carrying for several miles through the forest, make it relatively simple to locate the bird. Furthermore, many of the vocalisation recordings are taken from individual male birds that have habituated to human company (as for instance in Sherbrook Forest near Melbourne) and so allow very close proximity of humans during their courtship dance. By contrast,

magpie mimicry is sporadic and not tied to time of year or specific occasions. For this reason, it has remained difficult to document. Using recordings obtained by people at many separate locations in Australia, and doing so by drawing on a vast audience of listeners to Australia's most popular radio science program, it has been possible to document mimicry in wild Australian magpies.

The question remains: What is the function of mimicry? Why would birds deliberately transgress their species-specific sounds and move into the vocal territory of other species? It has been postulated that mimicry may be no more than a mistake in copying species-specific song correctly (Catchpole & Slater, 1995). This may be a possibility especially when closely related species (with somewhat different songs) hold nearby territories, but this option has to be ruled out for both the Australian magpie and for the lyrebird. At least in the case of the magpie, it was possible to show that mimicry practice is deliberate, selective and that the magpie responds to auditory stimuli external to its species. The very deliberate nature of the practice of certain mimicry types suggests that the mimicked type is intentionally learned and practised. A specific memory is established. The lyrebird renditions of mimicked sounds in specific sequences makes each mimicry type seem like a collector's item. Presumably, the male lyrebird's search for embellishments could have derived from its own song. However, as Figure 6 shows, the basic territorial song of the lyrebird is quite simple. While this song may be based on a genetically encoded template, the breeding song may have developed in response to sexual competition and it involves learning. The capacity to mimic in this species appears to have evolved over long periods of time.

Another hypothesis, that mimicry may result from selection for large song repertoires, has been in the literature for many years (see, for instance, Witchell, 1896). Both magpies and lyrebirds have exceptionally large repertoires and it could be argued that more 'mistakes' are therefore possible. Kroodsma and Pickert (1984) argued that for large song repertoires it was either impossible or costly to encode genetically very specific controls over which songs are learnt. There will thus be an increased probability of interspecific mimicry associated with selection (by any mechanism) for large song repertoires (Kroodsma & Pickert, 1984). There is some merit in this view. However, all this is ultimately saying is that basic qualities can be developed and enhanced through learning. The fact that both magpies and lyrebirds need to practise to retain the mimicked items should lead one to assess the mimicry in a positive rather than negative light- not as a mistake but as an acquired capability. Particularly the accuracy of the magpie's mimicked sounds ought to lead one to the conclusion that this

species has a very highly developed auditory perception and great musical discriminatory abilities.

Another hypothesis on mimicry deals with predation and mimicry. We know that insects may mimic appearance, smells and even light signals and dolphins and seals may use some vocal mimicry, but as far as is known to date, only birds mimic other species extensively in vocalisation. Purists argue that such mimicry by birds is not 'true' mimicry, 'true' mimicry being defined as having deceptive purposes useful for survival. Taking the models from studies of the insect world, 'true' mimicry involves three parties: the true identity of the mimicked one, say butterfly A, the mimicker called butterfly B, and the predator which is fooled by butterfly B (i.e., will not eat it because it looks like the unpalatable butterfly A). It is not clear why this model of mimicry should be binding for avian species. However, the literature still grapples with these issues and for good reason (Veerman, 1994). It is possible to conceive that a limited amount of the mimicry found in magpies might support the view that some avian mimicry is for the purpose of dealing with predators. Indeed, Robinson argued that mimicry was most likely to emerge in species exposed to predation (Robinson, 1975).

There has been no unambiguous evidence to date that birds mimic to avoid predation. However, it is possible that birds may mimic another to safeguard a territory. While this is not predation, such mimicry would also have clear survival function either in safeguarding a territory from a predator using a similar food chain as the species defending its territory, or by repelling a predator who may consider preying on the young in the nest. I have found evidence, only one recording respectively, of a wild magpie mimicking potential predators of their young, such as the barking owl and the boobook owl. Martine Hausberger, however, has noticed that starlings mimic predators in vain (personal communication, Rennes, July 2000). Apparently, the predators took no notice at all of the mimicry (see also Hausberger, Jenkins & Keene, 1991). The discovery that the Australian magpie also imitates two of potential predators of their young, the barking owl and the boobook owl, may add some credence to the view that mimicry may serve a function against predators, although it is not very strong evidence to date.

Some species mimic the calls of species that prey on them in order to teach their own young about the dangers. This has been noted in many species of the African Turdinae; when potential predators come close to their young, adults intersperse their own calls with mimicked calls of the predator (Oatley, 1971). The young may thereby learn the calls of the predator and so learn to avoid that species, although in this

case the mimicry may be used to drive off the predator rather than being a way of teaching the young to recognise the predator. There is no recorded evidence that Australian magpies incorporate mimicry in order to teach their offspring to recognise predators. However, in my research on vocal development of magpies at different nest-sites and throughout the dependent fledgling period, I observed that feeding parents sing to their offspring just before they feed. These observations were made on seven independent occasions. Parent and sibling were standing on the ground and, before the parent handed over the food to the offspring, it would sing a short phrase. Another example of this practice was found on the tapes of Carrick, Robinson and Falls (1965). This provided the only recorded example found of this practice involving mimicry. The female landed on the nest and mimicked the neighing of a horse before she fed the nestlings.

A third reason for mimicry, and the one most commonly cited, is related to the breeding season. Earlier studies on lyrebirds argue that mimicry is used purely as embellishment to increase chances of mating (Thoburn, 1978). Male lyrebirds certainly adorn their songs during breeding season with all manner of sounds, taken from the sound repertoire available to the male. This typically includes mimicry of other birds, the most distinctive ones being currawongs, kookaburras, yellow tailed black cockatoos and catbirds (mostly species which mimic others themselves). Sounds they include may also be barking dogs, car horns, creaking door hinges, car horns and even chain saws and many other animate and inanimate objects, all sound segments with which the bird will then liberally spice its own species-specific calls. It appears that lyrebirds sing their long sequences of mimicked calls to attract the female. It is as if they 'wear' the song component like trophies - the more elaborate and the more frequent the mimicry, the more the female may be impressed. Displays to outdo competition are common amongst polygamous and promiscuous males of class Aves. These vocalisations contain extremely beautiful musical sequences that are strung together to make a statement and attract a female (Robinson & Curtis, 1996).

Although this view of mimicry (embellishment) may explain the function of mimicry in the breeding song of the lyrebird it is not applicable to the Australian magpie since males do not sing solely to attract females. Further, phrases involving elements of mimicry in magpie song are highly variable. Unlike lyrebird breeding songs that are characterised by fixed patterns of sequence, the positioning and use of mimicry in magpie song appears to be arbitrary or, at least, highly complex.

Magpie song appears not to be organised sequentially. Magpie

mimicry is an integral part of song but, as the results have shown, the mimicked sounds are not random. Bird A might have mimicked visiting butcherbirds, occasional horses, cars, car horns, sirens, visiting cats and sounds of migratory birds. However, Bird A never utilised any of these sound sources. The only mimicked sounds stemmed from other long term aviary companions nearby and from constant sound companions of the captive magpie. These were budgerigars, peachface parrots (both species captive), kookaburras (rehabilitating), the dogs belonging to the property and humans (Table 1). To give an example. A juvenile butcherbird visited the aviary daily for a week, vocalising almost continuously. The rehabilitating magpie often joined in and sang a kind of duet with the butcherbird. Both in terms of purity of sound and in vocal range, the sounds of the grey butcherbird would be easily manageable for the magpie. However, Bird A never mimicked the butcherbird. By contrast, the convalescing kookaburra, too ill to vocalise much, vocalised only three times between April and June of 1996. Each of the vocalisations lasted less than a minute. The magpie mimicked the vocalisation after first exposure (of only less than a minute). A day after the 'laughing' sound of the kookaburra was first emitted, the magpie already fully incorporated this sequence into its own song. Moreover, as Figure 2 showed, the addition of a second kookaburra a little later and the first ensuing mimicry of that duet, increased practice of this mimicry which was retained for months thereafter.

The fact that the magpies included in this study seemed to mimic only sounds that were relevant and within their own territory suggests something about vocal learning in sedentary species. It is perhaps not so much a matter of the size of the repertoire as was argued before, but of social organisation (although the two are also often interlinked). A bird with a complex social organisation, as has the magpie, may require a map of its territory that is recorded not only visually but in an auditory fashion. This study found that mimicry in *Gymnorhina tibicen* is used exclusively for sound features belonging to inhabitants in the bird's own territory, as distinct from visitors to that territory.

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