THE FUNCTION OF VOCAL MIMICRY IN SOME AVIAN DISPLAYS

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SUMMARY

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Vocal mimicry in display is rare because specific identification is important. It occurs in the territorial displays of lyrebirds and bowerbirds and the reasons for this are examined. Its incorporation into the song of lyrebirds depends on the mimic using the model's calls at a time when they have no biological significance to the model and on the physical characteristics of the model's calls being significantly like those of the mimic to convey the same information to territorial rivals as do the mimic's own calls. The Noisy Scrub-bird mimics freely in sub-song but not in territorial song though it breeds in mid-winter. It has however an extended breeding season, which overlaps those of potential models, and unlike the lyrebirds males defend their territories throughout the year. Bowerbirds mimic the calls of predators simultaneously with their own territorial song to augment its aggressive nature. Mimicry is absent from the pre-copulatory display in all these species, where highly specific visual display predominates.

Mimicry of the vocalizations of one species during display by another is normally precluded by the need for specific identification. Consequently, though it often occurs in the sub-songs of passerines in which learning plays an important role in development of song, it is by no means a common feature of displays. Because sub-song appears to have little, if any, communicatory value this seems logical, but the dominant role of mimicry in the displays of some species is at first sight puzzling and has not hitherto been satisfactorily explained. Chisholm (1932, 1937) and Marshall (1950) reviewed the evidence but, as Marshall pointed out, their conclusions suffered from the lack of experimental data.

In this paper I shall report conclusions based on a comparative study of mimicry in the Atrichornithidae (scrub-birds), the Menuridae (lyrebirds) and the Ptilonorhynchidae (bowerbirds) to illustrate situations in which mimicry can play an important role in display.

The Menuridae present striking examples of the extensive use of mimicry in territorial displays. For about 80 per cent of its duration the song of the Superb Lyrebird *Menura novaehollandiae* consists of clearly identifiable calls borrowed from other species and although these are often modified and combined there is rarely any doubt about the identity of the model. The remaining 20 per cent consists of specific calls and a song that varies regionally. The song of *M. alberti*, however, contains only 70 per cent mimicry of other species and some 10 per cent of sounds that cannot be identified. The remaining 20 per cent is similar to that of *M. novaehollandiae* but regional variation is not so great. In both species males react to the replay of song by approaching the loudspeaker even when all lyrebird calls have been edited from the recording. In *M. novaehollandiae*, other birds such as Pilotbirds *Pycnoptilus floccosus*, Southern Yellow Robins *Eopsaltria australis* and White-browed Scrub Wrens *Sericornis frontalis*, which feed upon insects scratched from the litter by *M. novaehollandiae*, were also attracted to this edited tape, even when mimicry of their own calls had been removed from it. Specific identification is clearly no problem and is probably established by loudness, duration, the rapid succession of different calls and their modification to match the tonal quality of lyrebird song (Robinson MS).

Males of the Menuridae defend territories of three hectares or more and are separated from rival males in dense forest by distances up to one kilometre. They display on the ground at arenas and occasionally on a large log or rock. Song also may be given from a branch of a tree, particularly at dawn or dusk, but they cannot display there because the display is elaborate and involves much turning and posturing. The dense vegetation at ground-level prevents birds seeing each other at distances of more than two or three metres and consequently loud continuous and strongly directional song appears to be used to provide rival males and prospective mates with information regarding the extent of the territory and the location of the singer. This information is also available to predators and the frequent occurrence of alarm-calls in the song suggests that the levels of the patterns of advance and withdrawal are continuously varying. Such a situation favours the emergence of mimicry in song (Robinson MS) but does not explain its dominant role in the songs of the Menuridae.

Both *M. alberti* and *M. novaehollandiae* breed in winter and during the breeding period the calls mimicked have no biological significance for the models because they are not breeding, and, though

both Lyrebirds mimic many sounds in sub-song, mimicry in territorial song is limited to the calls of those species that do not breed at the same time (Robinson MS). For example, *M. alberti* does not mimic the Eastern Whipbird *Psophodes olivaceus*, which is an early breeder in rainforest, nor do individuals of *M.novaehollandiae* in the same conditions. In almost all other parts of its range, however, *M. novaehollandiae* mimics the Whipbird freely because the breeding seasons of the two species do not as a rule overlap. *Atrichornis clamosus*, another ground-dwelling species in dense vegetation, does not mimic in territorial or courtship display although it breeds in winter. It has, however, a second breeding peak in September when most other species in the area are also breeding and significantly males of *A. clamosus*, unlike the Menuridae, defend their territories throughout the year. Consequently mimicry is absent from its territorial display.

Location, dominance and individual identification are important in territorial display and the Menuridae have many sounds that they can use for these purposes. Spectrographic examination of the sounds used by them in territorial display shows that all are strongly directional. In addition they mimic by preference the calls of large noisy, and often agressive, arboreal species such as the Black Cockatoo *Calyptorhynchus funereus*, the Red Wattlebird *Anthochaera carunculata* and the Pied Currawong *Strepera graculina*, and the loud territorial songs of the Grey Shrike-Thrush *Colluricincla harmonica*. Observation of these species has shown that they will readily attack members of their own or other species in territorial defence or in defence of the nest-site. Though the preferences vary considerably in different habitats such loud and aggressive calls account for more than 90 per cent of the mimicry of *M. novaehollandiae* throughout its range. *M. alberti* is rather more restricted in its choice of models owing to the coincidence of breeding seasons but similarly prefers the calls of *C. harmonica* and other loud or aggressive calls such as those of the Crimson Rosella *Platycercus elegans* and the Satin Bowerbird *Ptilonorhynchus violaceus*, which account for some 80 per cent of its mimicry.

P. violaceus mimics in courtship display in a rather unusual manner. This display takes place on the ground at the bower, which is decorated with flowers and other bright objects, and the male himself is iridescent blue with flashing violet eyes. The accompanying song, however, though very harsh, is quite subdued and lacks directional clues, perhaps as a consequence of the danger of predation caused by long periods of display at the bower. The threatening nature of the display is reinforced at times by mimicry of the Kookaburra *Dacelo gigas* and the Raven *Corvus coronoides*, both of which are predators of eggs and young. These calls are given simultaneously with the song and at a very low level, which suggests that the model is at a distance. Mimicry stops before copulation and is replaced by a specific call. Similar mimicry of predators has been noted by Marshall (1950) in other members of the Ptilonorhynchidae.

Even in dense vegetation visual signals are effective in pre-copulatory displays and striking displays are characteristic of the Atrichornithidae, Menuridae and Ptilonorhynchidae; so, it is not surprising that mimicry is replaced before copulation by highly specific sounds. *A. rufescens*, which mimics quite freely in some other circumstances, does not do so in pre-copulatory display and nor does *A. clamosus*. When a female of *M. novaehollandiae* approaches a singing male specific sounds gradually displace mimicry; the song becomes quieter and mimicry of small birds such as *S. frontalis* often occurs. This is then superseded by a specific clicking sound that may last for as much as five minutes and precedes copulation (Watson 1965; Kenyon 1972).

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