

in the growth rate and increase of 4% in the asymptote approximates the differences cited by Oniki & Ricklefs (1981) when they compared growth data analysed by the two methods.

The growth rate of the sunbird is 5% slower than the average of 30 small (< 100 g) tropical passerines, $K = 0.387 \pm 0.079$ (Ricklefs 1976) and is within one standard deviation of the mean of that sample. Its growth rate is 25% slower than the average of nine tropical passerines, $K = 0.461 \pm 0.060$, from Manaus, Brazil (Oniki & Ricklefs 1981) and the difference is significant by *t*-test ($t = 2.822$, $P < 0.05$, $df = 11$). While it is also well below average ($K = 0.502 \pm 0.071$) of 51 temperate passerines (Ricklefs 1976) it is not significantly different ($t = 1.82$, $P > 0.05$) from that sample by *t*-test (Sokal & Rohlf 1969, p. 223), thus the Yellow-bellied Sunbird does not appear to grow significantly more slowly than temperate zone passerines.

Its growth and development, although slower, is very similar to that of the Brown-backed Honeyeater and resembles that of arctic and temperate passerines that have been studied in detail (see Maher 1986). The problem of clarifying the adaptations of growth and development of tropical passerine birds compared with temperate and arctic zone passerines requires more study of differential growth in addition to studies of weight gain.

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Phatic Communication in Bird Song

F. Norman Robinson

56/7 Harman Rd, Sorrento, W.A. 6020

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Complexity and diversity in bird song have provoked many hypotheses from the Anti-monotony Principle (Hartshorne 1956) to the Beau Geste Hypothesis (Krebs 1977). Studies of the vocal displays of the lyrebirds (Menuridae) (Robinson 1974, 1975, 1977) led to an examination of vocal mimicry in the sub-song of the Australian Magpie *Gymnorhina tibicen*. These studies sug-

gested that vocal mimicry could be a means of expressing sociability rather than communicating a specific meaning. The term phatic is used to describe this function in speech (Sykes 1985) and was used to explain the function of vocal mimicry in the song of the Superb Lyrebird *Menura novaehollandiae* (Robinson 1977). It is now proposed that it could have wider application.

The vocal displays of the lyrebirds

Both the Superb Lyrebird and Albert's Lyrebird *M. alberti* have spectacular visual displays that complement a form of dispersed lek behaviour involving a number of courts in large territories (Curtis 1972; Robinson & Frith 1981). Prolonged visual and vocal displays are performed by males mainly at these courts (Watson 1965; Kenyon 1972; Lill 1979; Robinson & Frith 1981).

The vocal displays consist of a continuous stream of mimicry interspersed with specific signals indicating the presence of a predator or some other disturbing factor, the presence of a conspecific of either sex, the onset of copulation, or a territorial song that is usually answered by a neighbouring male or males (Fig. 1). In a species that does not exhibit any signs of interspecific aggression it has no meaning for the models because they recognise the mimic as a lyrebird (Robinson 1974).

Superb Lyrebirds breed in winter when the weather is cold and wet, with snow at the higher altitudes. Measurement of the songs and calls of the models (Robinson 1975) showed that they are minimal in July and August when young Superb Lyrebirds are exposed to loud and continuous song and mimicry from adult males for a daily maximum of more than four hours (Robinson & Frith 1981). Consequently, they learn the mimicked sounds from adult male Superb Lyrebirds rather than from the models (Robinson 1974, 1975; Bell 1975). Mimicry can subsequently be reinforced by hearing the models and individuals may add to or subtract from the repertoire but its structure is basically conservative and

attempts to add to the repertoire of Superb Lyrebirds at Tidbinbilla by replaying calls of the Eastern Whipbird *Psophodes olivaceus* were unsuccessful (Robinson 1975).

When Superb Lyrebirds were introduced to Tasmania from Victoria in 1934, their songs included calls of the Eastern Whipbird which is absent from that island (Sharland 1944). Analysis of a recording made in 1964 showed that this call still formed part of the repertoire and that the calls of some Tasmanian endemics had been added (Wall & Wheeler 1966).

The vocal display of Albert's Lyrebird is similar but the number of models used is restricted since the breeding season overlaps that of many of the available models. In both species at least 70% of the vocal display is mimicry (Robinson 1974, 1975).

The sub-song of the Australian Magpie

Male Australian Magpies mimic only in sub-song. When the young have left the nest adult males begin to moult and produce a prolonged and continuous sub-song that contains a variety of mimicked calls of other species combined with their own subdued calls. This is in marked contrast to their breeding behaviour when family groups defend territories by aggressive visual and vocal displays restricted to specific informative signals. Moulting males skulk in cover but are never far from the rest of the group with which the sub-song provides a social contact without expressing alarm, aggression or courtship (Robinson 1975). Such mimicry oc-

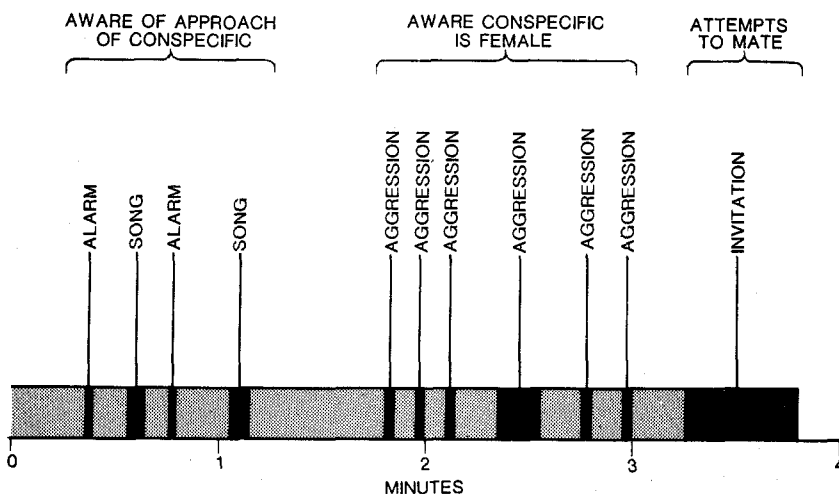


Figure 1 A sample of male Superb Lyrebird vocal display at Tidbinbilla leading up to attempted mating. Mimicry is shown as stippled black and specific signals as solid black.

curs in the sub-song of many Australian passerines (Chisholm 1932, 1937).

Discussion

Dawson (1982), in a review of attempts to explain the complexity and diversity of bird song, concluded that no one hypothesis adequately explained the evolution of repertoires. These hypotheses are based on the assumption that song responds to the immediate needs of reproduction. Such emphasis has excluded the possibility that birds may have a need for sociability for its own sake and that this need may be much stronger in some species than in others.

Male lyrebirds in their dispersed lek situation are widely separated from one another and their very loud song can be heard at distances of up to one kilometre. Each geographically isolated group has its own distinctive song. Outside the breeding season groups may be seen together. The song and calls in the vocal display are simple and are easily distinguished from the very complex mimicry that forms a non-threatening unimportant subject that can keep the lines of communication open.

Hindmarsh (1986), after a comprehensive study, came to the conclusion that there was probably no functional explanation for mimicry in the song of the Common Starling *Sturnus vulgaris*, that it was simply part of the song and that this feature of passerine song had no evolutionary significance. He further suggested that if this were the case then other aspects of song variation might also be non-functional.

The function of sub-song in early song learning has been clearly demonstrated but the functional significance of its repetition in later years, after the patterns of adult singing are set, has not been satisfactorily explained (Marler & Peters 1982).

If sociability is the function of mimicry in song and in adult sub-song, it follows that it is more likely to occur in species where the social group is important and when males are isolated from the group. This is certainly the case with lyrebird and Common Starling songs and with the sub-song of adult Australian Magpies.

Conclusion

It is unlikely that lyrebirds should spend up to three hours of their day in producing very loud signals to no purpose, nor does it seem likely that other mimics

should waste energy in this way during the breeding season or even in adult sub-song.

A need for social contact appears to be a logical reason for the use of mimicry and, for those species that are precluded from its use, diversity or complexity in song may have evolved to meet this need. Adult sub-song itself, with or without mimicry, may also have evolved for this purpose. The social group can be an important element in survival and phatic communication may be a means of reinforcing the social bond.

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