

## Regional Variation in the Territorial Songs of Superb Lyrebirds in the Central Tablelands of New South Wales

Vicki Powys

'Snowline', Sunny Corner, NSW 2795

**Summary:** A seven year study of territorial songs of the Superb Lyrebird *Menura novaehollandiae* in the Central Tablelands of New South Wales found clear evidence of regional song variation. Songs were locationally distinct and did not vary in structure in seven years. Twelve different dialect groups were found within a 35 km radius, each of which comprised from 5-50 or more singing males in native forest habitats. Groups were reliably identified according to their

songs and no evidence of migration was found. Regional variation in song was greatest in geographically separated habitats but song variation was still apparent at locations only 5 km apart in acoustically isolated gullies. Some groups used only one territorial song but other groups consistently used up to three different songs and sometimes combined them. Mimicry was incorporated into some songs. The songs of seven groups are compared and described.

The Superb Lyrebird *Menura novaehollandiae* is endemic to Australia and occurs in native forests in the south-east of the continent along both sides of the Great Dividing Range, from the New South Wales–Queensland border region to southern Victoria, with an introduced population in Tasmania (Blakers et al. 1984).

Male Superb Lyrebirds are well known for spectacular vocal displays that occur during the winter breeding cycle and include loud and sustained bouts of bird-call mimicry. Less well known are the equally loud territorial songs of about ten seconds duration that occur regularly within this stream of mimicry. These songs are directed by male lyrebirds towards answering rival males and therefore correspond in their territorial intent with the breeding songs of most passerine bird species. Lyrebird populations occur in aggregations and geographically or acoustically isolated groups have locationally distinct songs known as dialects.

Regional dialects are known to exist in passerine birdsong generally and Superb Lyrebird territorial song has been shown to vary significantly in structure throughout the entire range of the species (Wall & Wheeler 1966; Robinson 1974, 1975; Bell 1976; Reilly 1988; Robinson & Curtis 1996). Why such major regional differences in lyrebird territorial songs should occur is unclear. Variation over a smaller geographical scale is less well documented; Robinson & Curtis (1994) have found eight distinct song dialects over a 35 km radius in the Stanthorpe–Tenterfield area of New South Wales, although Taylor (1986) found little regional variation within a study area of 35 km radius in the Australian Capital Territory. Most lyrebird studies have

concentrated on mimicry or behaviour, with few comparative analyses of song variation.

It is generally agreed that Superb Lyrebird song may take many years to evolve and change, and that both song and mimicry are passed from one generation to another with immature birds learning from adult males. It is also known that lyrebirds are weak fliers and probably do not travel great distances within their estimated 20 year lifespan, one long distance record for a banded lyrebird being 10 km (Reilly 1988). This relative lack of mobility in lyrebirds suggests that any dissemination of songs over a wide area would be a slow and gradual process.

While some individual territorial songs have already been described in the literature, the constancy of those songs and the occurrence of song groups has not yet been demonstrated. From an intensive long-term study of regional song variation within a relatively small geographic area I show the structural, locational and temporal constancy of territorial song in Superb Lyrebirds. Specifically, I will show that a group of these birds in any one area of the Central Tablelands of New South Wales can, over a span of many years, be identified by analysis of the particular territorial song or songs of that group.

This study began as an exercise to seek out Superb Lyrebird populations in my home area, to monitor and compare their songs and to look for any changes in song or movements in population over many years. The presence of song groups was established, but the study was made more complex when it was found that in some locations several different songs were in evidence, contrary to the accepted view that only one terri-

torial song type is used within any one population group. Of additional interest is the 5-10 second pattern of introductory mimicry that preceded some of the songs, and the fact that mimicry was incorporated into some songs.

### Study area and methods

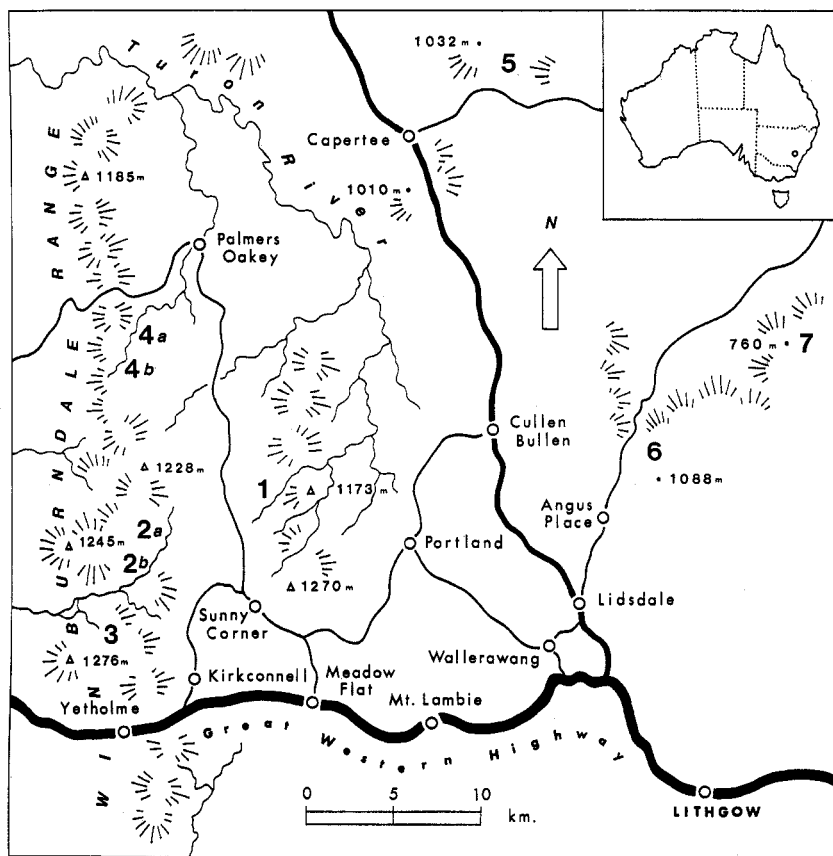
For this study, I recorded Superb Lyrebirds calling at seven different locations in the Central Tablelands of NSW, over a seven year period. All locations were within a 35 km radius of Sunny Corner (33°23'S, 149°43'E), 30 km east of Bathurst, in an area that has not been previously studied (Fig. 1).

The study area encompasses rural clearings and pine plantations, with native eucalypt forest comprising roughly 40% of the total land area shown in Figure 1. The search for Superb Lyrebird populations was restricted to native forest which represents the only viable

habitat for this cryptic and ground-foraging species.

Superb Lyrebird song can be heard from up to 1 km away enabling a wide area to be aurally surveyed from fire trails and roads. Twenty different areas of native forest were sampled for lyrebird presence (as evidenced by song) during the May–July breeding season, from 1988 to 1994. Groups of calling lyrebirds were located at 12 of the 20 locations, and seven of those groups were chosen for this study due to their relatively strong calling populations (locations 1-7). These groups remained in the same locations from year to year and their songs were monitored in 1988, 1991 and 1994. Each of the five additional song groups located in the Winburndale Ranges had a distinctive song and a fixed territory but continuous monitoring proved difficult due to less frequent calling from small populations and/or access problems.

The study area shown in Figure 1 covers two significantly different geographical areas. Locations 1-4 are in



**Figure 1** Location map. 1, Blackbutt Mountain; 2a & 2b, Lagoon Creek; 3, Eskdale Gulf; 4a & 4b, Palmer's Oakey Creek; 5, Mt. Airly; 6, Blackfellows' Hands; 7, Glow-worm Tunnels.

**Table 1** Recording dates, and number of calling male Superb Lyrebirds within 1.5 km radius at seven locations within 35 km of Sunny Corner, near Bathurst, New South Wales.

Location	1988-89		1991		1994	
	Date	No. of birds	Date	No. of birds	Date	No. of birds
1. Blackbutt Mt.	24.6	10	13.6	10	11.6	10
2a. Lagoon Creek	23.6	6-10	19.6	6-10	13.6	6-10
2b. Lagoon Ck. sth	—	—	—	—	4.6	10
3. Eskdale Gulf	—	—	2.7	7	8.6	5
4a. Palmer's Oakey Ck.	25.6	10	16.6	10	28.5	10
4b. Palmer's O. Ck. sth.	25.6	10	18.6	10	28.5	0
5. Mt. Airly	23.2	5	14.6	15-20	1.6	10
6. Blackfellows Hnds.	13.7	20	25.6	50	9.6	20
7. Glow-worm Tunnels	—	—	—	—	7.7	20

the Winburndale Ranges, whereas locations 5-7 are within the Blue Mountains sandstone country.

The Winburndale Range is steeply undulating, averaging 1000 m asl, with geologically complex rock strata dissected by numerous creeks. The stoney soils support a dry sclerophyll forest with acacia understorey.

Blue Mountains landforms are horizontally bedded, eroding to form sheer sandstone cliffs, caves and pagoda formations, and average less than 1000 m asl. Creeks and water seepages sustain many fern species, including tree ferns, and the deep sandy soils support a dry sclerophyll forest with diverse heathland and acacia understorey.

Locations 2, 3 and 4 are linked by continuous native forest habitat, but location 1 is separated from them by a pine plantation. Locations 5, 6 and 7 are also linked by continuous native habitat but open farmland separates them from locations 1-4. Therefore, the Winburndale locations are geographically isolated from the Blue Mountains sandstone locations. Superb Lyrebirds may sometimes use mature pine plantations as corridors between areas of native forest but open farmland presents a definite barrier because lyrebirds are not likely to travel across large cleared tracts of country.

Recordings were made in 1988 using an Aiwa microcassette recorder with tie-pin microphone. In 1989 a Sony Walkman WMD6C was used at one location, and in 1991 and 1994 recordings were made with a Sony TCD D10 PRO DAT machine with ECM MS5 stereo microphone. In all cases, singing birds were stalked to within recording range (3-20 metres). Individual selection was random and also depended on luck; immediate

cessation of song occurred if these shy and wary birds became aware of my presence.

At each location, where possible, at least two different birds were recorded on any one visit. As all birds were unmarked, it is not known if the same two individuals were recorded from year to year. However, this was considered to be unlikely, with five to twenty or more singing males at any one locality from which to choose (Table 1). Continuous recorded sequences for any specific male averaged around seven minutes and were often much longer.

A total of about eight hours of repertoire was recorded, from which over 500 territorial songs were analysed (Table 2). Audiograms of representative songs were made using the AUDIOGRAPH program v2.0.2 of Ralph Sutherland, Canberra, on a Macintosh Centris 610 computer, MacRecorder and SOUNDEDIT PRO (Figs 2-8).

### Terms

The following terms are used in this paper.

*Repertoire* All the sounds produced by a singing lyrebird, including territorial song (which varies regionally), mimicry (of local bird species), plus various whirring, clicking and *billick* calls that are common to all Superb Lyrebirds across their entire range.

*Mimicry* Vocal copying of avian songs, calls, beak snapping and wing beats. These mimicked sounds are often linked together in random fashion to produce a loud and continuing stream of sound.

*Territorial song* A loud and recurring specific song of 5-10 seconds duration that usually occurs with-

**Table 2** Territorial song analysis data from Superb Lyrebird recordings listed in Table 1.

Location	Study period	No. of song types	Song type used	%	Av. song rate/minute in repertoire	No. of songs analysed	From no. of birds
1	1988-94	1	A	100	1.0	94	15
2a	1988-94	3	B-C-D	17	0.9	70	5
			B-D	6			
			C-D	19			
			C	27			
			D	31			
2b	1994	3	B-C-D	0	0.9	96	5
			B-D	14			
			C-D	0			
			C	36			
			D	47			
3	1991-94	3	E-G	7	0.6	83	4
			F	47			
			G	46			
4a & 4b	1988-94	3	H-(lorJ)	19	1.7	94	15
			l or J	81			
5	1989-94	2	K	50	0.7	57	6
			L	50			
6	1988-94	1	M	100	0.7	64	6
7	1994	1	N	100	0.6	10	2

in the stream of mimicry; but sometimes alone. The song may include recognisable elements of mimicry, but mixed together in such a way as to produce a unique blend that remains consistent each time the bird calls. This song is used by a male to proclaim territory and is usually answered by neighbouring males. Territorial songs vary considerably over the distribution range of the Superb Lyrebird and these differences in song are sometimes referred to as dialects.

*Song group* Aggregations of lyrebirds that share the same locational dialect of territorial song. The term 'group' is used in this paper for convenience, without necessarily implying any social interaction.

### Abbreviations

Territorial songs are fully described and the different phrases numbered i-vi, in the captions that accompany the audiograms. Mimicry has often been incorporated into the songs and, for the sake of simplicity, names of commonly mimicked species and their calls are abbreviated as follows:

HE = loud *chew*, *chop* or *chickup* notes of White-eared and Yellow-faced Honeyeaters *Lichenostomus leucotis* and *Lichenostomus chrysops*.

GST = Grey Shrike-thrush *Colluricincla harmonica* (song phrases are also accompanied by mimicked beak clapping).

YMag = food begging calls of young Australian Magpie *Gymnorhina tibicen*.

RWB = Red Wattlebird *Anthochaera carunculata* (harsh *kark-aka-kark* calls).

CRos = Crimson Rosella *Platycercus elegans*.

Kooka = Laughing Kookaburra *Dacelo novaeguineae* laugh-prelude (a half-hearted, harsh chuckle).

## Results

### Lyrebirds in song groups

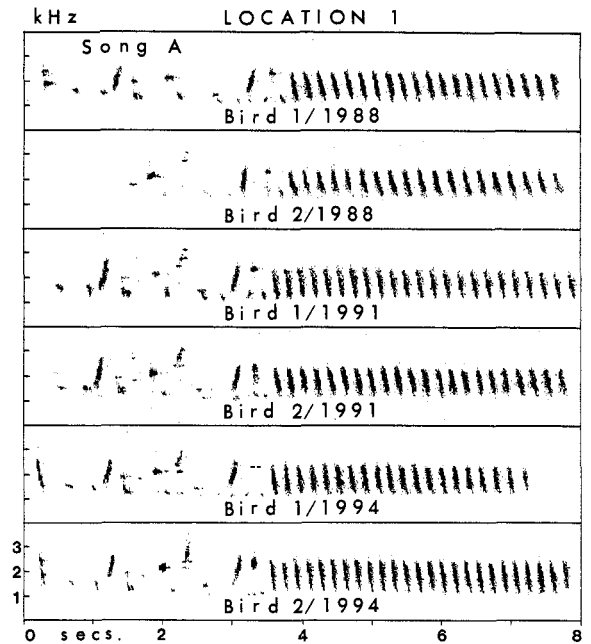
Calling male Superb Lyrebirds were not evenly spread throughout native forest areas, but instead occurred in groups. Lyrebirds on the Winburndale Ranges favoured sheltered gullies close to streams and none was heard on the drier plateaus; so they were grouped according to song type, in gully areas (locations 1-4). In the Blue Mountains sandstone habitats (locations 5-7), calling lyrebirds were located in gullies and also on plateaus and hillsides, indicating a more widely suitable breed-

**Figure 2** Blackbutt Mountain (location 1). Audiograms show Song A (ii-iii\*). Only one territorial song type was used at this location; it was remarkably consistent for all individuals over the study period. Analysis of the one variable component, (number of *chews* per Aiii) showed the average in 1988 was 16, in 1991 it was 23 and in 1994, 19.

*Song description*

*Song A* (nearly always preceded by Kooka): (i) 2-3 HE notes; (ii) GST-based phrasing which did not vary between individuals; (iii) series of 9-37 vigorous *chews* similar to a Rufous Whistler *Pachycephala rufiventris*; and (iv) CROs *ark-ark* (usually).

[\* these roman figures refer to the phrases described in the Song Descriptions lower in the captions]



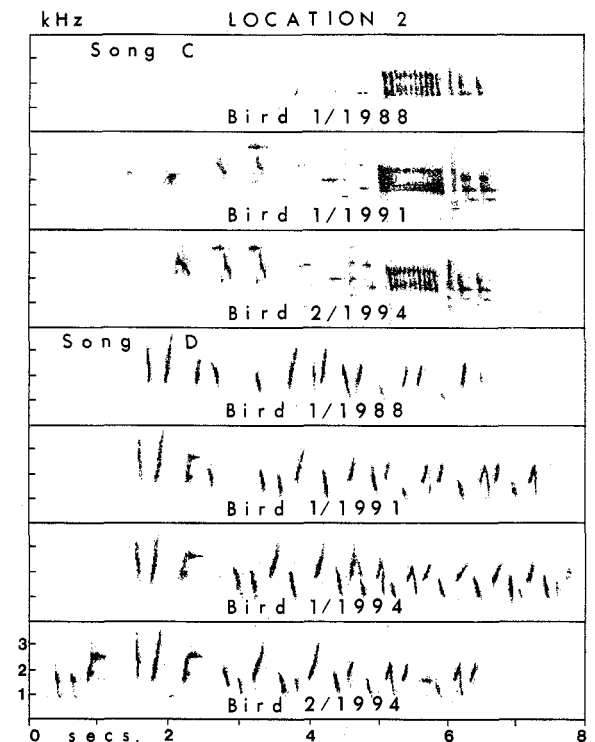
**Figure 3** Lagoon Creek (location 2). Audiograms show Songs C (i-iv) and D (iii-iv). Three different territorial songs were used at this location, with little variation over the study period. Songs B (Fig. 6) and C were somewhat similar to Eskdale Gulf (location 3) songs, while Song D was unique to Lagoon Creek. Songs B, C and D are shown in the audiograms as separate songs, however they also occurred in various combinations as shown in Table 2. These combination patterns did not alter at location 2a over the study period. At location 2b (2-3 km from 2a along the same creek) the song content was very similar to 2a in 1994, but the combination patterns were markedly different, as can be seen in Table 2.

*Song description*

*Song B* (see Fig. 6) (i) soft and melodious series of six quacking notes, lasting 5 s. Sometimes preceded by 2-5 soft descending whistles.

*Song C* (always preceded by YMag when song started at C). (i) 2-4 HE notes; (ii) 4 RWB notes (in 1988) OR 4 melodious notes (in 1991 & 1994); (iii) loud vibrating note of 1 s duration; (iv) 3-4 RWB notes (not if C-D or B-C-D)

*Song D* (often preceded by Kooka or YMag when song started at D). (i) 2 HE notes or 4 RWB notes; (ii) soft *parp-parp*; (iii) 1-3 variable GST phrases; (iv) series of variable GST-based *we-o-tos* and/or *we-o-we-t-dos*, sometimes stuttering on the 't's. The series fades to an indecisive finish. This part of the song emphasised the lower pitched notes of *to-do*, thus varying from the higher pitched bell-like *weeta* notes of Eskdale Gulf (location 3). When Song D is preceded by Songs C or B-C, parts (i), (ii) and (iii) are omitted.



**Figure 4** Eskdale Gulf (location 3). Audiograms show Songs F (i-iv) and G (iii-vi). Three different territorial songs were used at this location, with little variation over the study period. Songs F and G were in equal and frequent use, while Song E was used only occasionally, and always in combination E-G. Songs E and F were somewhat similar to Lagoon Creek songs, while Song G was unique to Eskdale Gulf. Song type usage is shown in Table 2.

#### Song description

**Song E** (see Fig. 6). (i) soft and melodious series of 5-6 quacking notes lasting 5 s, similar to but not the same as for Lagoon Creek (location 2). Sometimes preceded by 2-5 soft descending whistles.

**Song F** (always preceded by YMag). (i) 2-3 HE notes; (ii) 4 RWB notes; (iii) loud vibrating note of 1 second duration; (iv) 4 RWB notes.

**Song G** (often preceded by Kooka). (i) 2 HE notes; (ii) soft *parp-parp* (sometimes omitted); (iii) 1 variable GST phrase; (iv) short trill (used occasionally in 1991 and frequently in 1994); (v) GST-based short series of *we-o-we-tos*; (vi) series of loud and rapid *weeta* notes (5-19), averaging 7 in number, fading to an indecisive finish. These *weeta* notes were far-carrying and bell-like when heard from a distance.

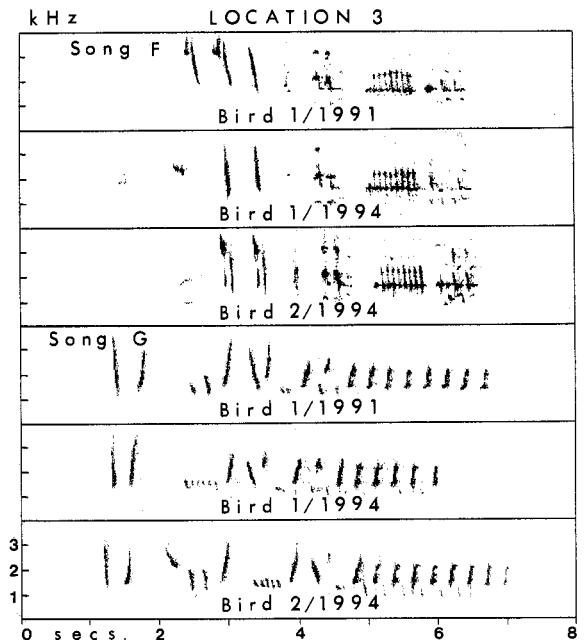
ing habitat, although some selectivity of habitat was still apparent (Fig. 1).

#### Size of groups

In locations 1-4, song groups did not extend beyond 2-3 km, but in locations 5-7 populations were larger and the extent of each song group was unknown. Locations 2a-2b and 4a-4b shown in Figure 1 represent sub-populations within two different song groups. Table 1 shows the number of calling male lyrebirds within a 1.5 km radius at each location studied. A count was made of the number of calling lyrebirds that could be heard singing in late afternoon during the breeding season. Coverage was made from a traversed line of 0.5-1.0 km within each population group. The reduction in numbers in 1994 probably reflects diminished calling due to drought, rather than an actual loss of birds.

#### Locationally distinct songs

Song samples in the form of audiograms are given for seven locations, each spanning a period of up to seven years, as shown in Figures 2-8. The audiograms show that individuals within each group used the same song or songs, and that the songs from each location have remained unchanged for a period of four to seven years. Song groups did not migrate, so that a particular song



or songs could be identified with a particular locality, over the study period.

At any one location, minor variations occurred in songs, but there was as much song variation from any one bird as there was between several different birds so that identification of individuals from their song characteristics was not possible.

Outside the breeding season, singing was much less sustained or even non-existent, but when heard, the territorial songs did not appear to vary throughout the year. A recording made in summer of 1989 at Mt. Airly (location 5), is illustrated in Figure 7 and shows that the two territorial songs of Bird 1/1989 were consistent with the winter breeding songs of that group, in 1991 and 1994.

#### Regional song variation

Audiograms in Figures 2-8 show considerable regional variation in the territorial songs. However, where habitat continuity occurred, there was also some correlation of song type. This is evidenced in partial similarities in the songs of the Winburndale Ranges (locations 1-4), and also in a similarity of songs within the sandstone country (locations 5-7). Where habitats were discontinuous the songs were also dissimilar, so that Winburndale Ranges songs were markedly different from sand-

**Figure 5** Palmer's Oakey Creek (Location 4). Audiograms show Songs I (ii-iv) and J (ii-iv). Three different territorial songs were used along a 3 km stretch of this creek, and did not change over the study period. Abbreviated versions of Songs I and J were also used, more so in 1991 and 1994 than in 1988. Song H was used only occasionally, and was always followed by Songs I or J. In 1988 several individuals used both Songs I and J in their repertoire. In 1991, either I or J was used, with birds using Song I grouped at the south end of the creek (location 4b) and those using Song J at the north end (location 4a). In 1994, north end birds continued to use Song J, with no calling birds at the south end (possibly due to drought). Songs I and J had some similarities to other songs in the Winburndale Ranges, but their endings were distinctive and unique.

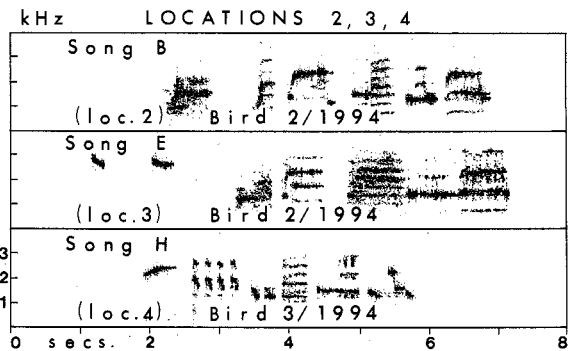
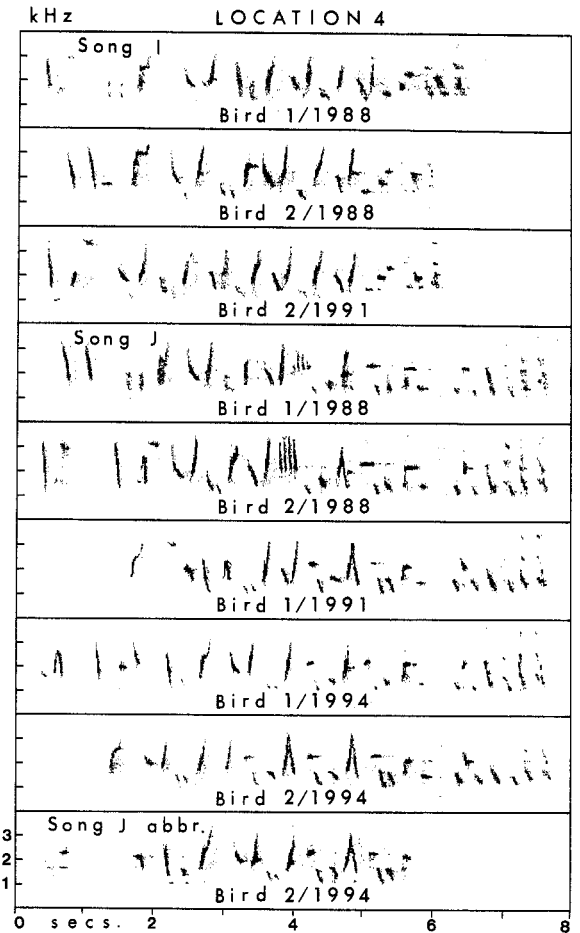
*Song description*

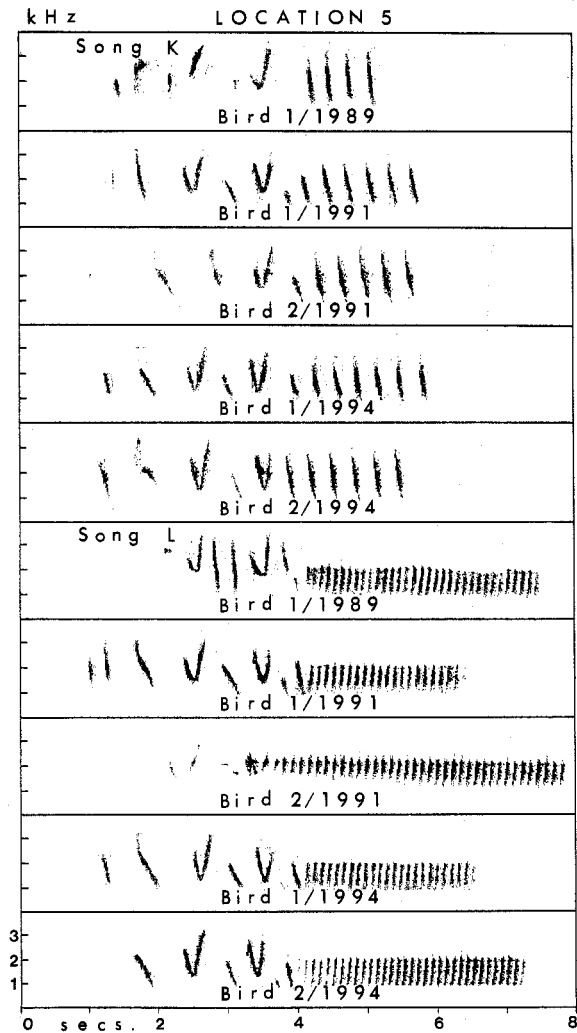
*Song H* (see Fig. 6) (always preceded by a pause in repertoire). (i) 2-4 soft ascending or descending whistles; (ii) descending series of up to nine *parp* notes in three groups; (iii) melodious *wah-teedle-do*.

*Song I* (often preceded by YMag or Kooka). (i) 2-3 HE notes (sometimes omitted) (ii) 1-3 variable GST phrases; (iii) GST-based series of 3-5 *we-to-we-tos* with emphasis on *we*; (iv) distinctive ending of five notes in uneven metre, combining melodious and quacking notes. This ending is omitted in abbreviated version of Song I.

*Song J* (often preceded by YMag or Kooka). (i) 2-3 HE notes (sometimes omitted); (ii) 1-3 variable GST phrases; (iii) variable series of 3-5 *we-to-we-tos* commencing as for I(iii), but then shifting emphasis to *to*'s, thus changing the metre; (iv) distinctive ending of 10 notes, both melodious and quacking, some with double-note effect as if GST and RWB had called simultaneously. In abbreviated version of J, the song ends on the first of these 10 notes. When Song J is preceded by Song H, parts (i), (ii) and sometimes (iii) are omitted.

**Figure 6** Audiograms from locations 2, 3 and 4, showing Songs B(i), E(i) and H(i-iii). Songs B and E were quite similar, while H was different, nevertheless these three Winburndale songs were clearly related in that they always occurred as the first song in a combination of two or three songs and they were all very soft songs. The songs were consistent over seven years but only one example of each is shown. The song volume was artificially boosted to produce the audiograms.



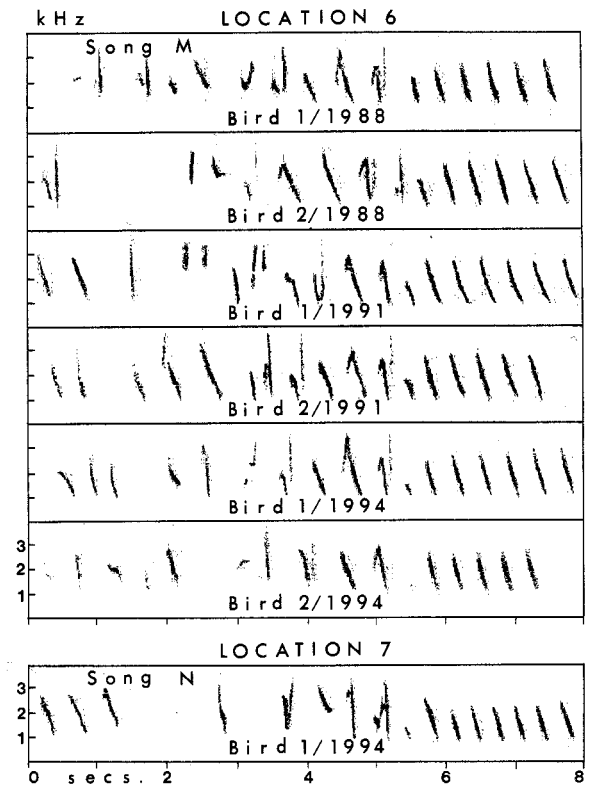


**Figure 7** Mt. Airly (location 5). Audiograms show Songs K (i-ii) & L (i-ii). Two different territorial songs were in equal use and did not change over the study period. Although often preceded by mimicry, no mimicry was incorporated into these songs, which consisted of the lyrebird's own calls. Song K was similar to the songs of locations 6 and 7, while Song L was unique to the Mt. Airly region. The two songs were never combined.

*Song description*

*Song K* (often preceded by GST phrase or CROs bell-like call). (i) about 3 s of loud whistled sliding notes, both ascending and descending, somewhat variable and punctuated with several *chip* notes; (ii) a series of 3-7 evenly spaced loud descending *chews*, about 3 per s.

*Song L* (preceded by same mimicry as for K). (i) as for K(i); (ii) a loud liquid trill lasting on average 3 s, with 10 notes per second. This song carried well over a distance.



**Figure 8** Blackfellows' Hands (location 6); Glow-worm Tunnels (location 7). Audiograms show Songs M (i-ii) and N (i-ii). One type of territorial song was used at location 6, and did not change over the study period. Unlike locations 1-5, GST mimicry was seldom used in song or repertoire. The song consisted of the lyrebird's own calls, punctuated by brief snippets of mimicry, and the mimicry that preceded the song appeared to be random. The song sample from location 7 is included for comparison with similar songs from locations 5 and 6. Only one song type was used at location 7, and GST mimicry was minimal in both song and repertoire.

*Song descriptions*

*Song M*. (i) variable series of loud, slow, mostly descending notes, punctuated by *chips* and snippets of mimicry, lasting on average 7 s; (ii) series of 4-16 (average 6) evenly spaced loud descending *chews*, at the rate of 3 per s.

*Song N*. (i) variations of loud, slow, mostly descending notes, punctuated by snippets of other sounds, lasting about 7 s. Similar to location 6 but with somewhat more variety of sound.; (ii) series of 5-10 (average 7) evenly spaced loud descending *chews* at the rate of 3 per s.



stone country songs. No obvious link could be found to connect song type with habitat structure.

Winburndale Ranges songs made considerable use of mimicry in their structure, incorporating Grey Shrike-thrush and Red Wattlebird calls. Sandstone country songs rarely incorporated mimicry and instead consisted of the lyrebird's own calls.

Songs in common usage in the Winburndale Ranges did not extend beyond 10 km, and regional variation occurred between populations only 5 km apart. However, the very similar song types K, M and N that occurred in the sandstone areas extended over a distance of at least 25 km with only minor variations.

### Multiple song use

At four of the seven locations in this study, two or three different territorial songs were in regular use, as shown in Table 2 and also in Figures 3-6. Robinson & Curtis (1996) have observed that male Superb Lyrebirds in the Sundown National Park of Queensland normally used only one song, but combined two different regional songs when confronting one another. Where multiple song use occurred in my study area, the different songs were used equally and frequently over a period of time, and thus appeared to be permanently fixed into the repertoire. Such multiple song use in lyrebirds has not previously been described.

### Song combinations

At the locations where multiple song use occurred, these songs were sometimes combined. Set patterns were apparent in these combinations, and the songs and combinations were common to all the calling birds in each group, showing little or no change over a seven year period. The percentage of use of each combination is shown in Table 2. Examples of songs that were used in combinations are shown in Figures 3-6. Combined songs have not been illustrated due to their much greater length (up to 14 s long), but their use is fully described in the captions.

### Song rate within repertoire

The repertoire at all locations comprised mainly a continuous stream of mimicry, with territorial songs occurring at regular intervals ranging from 0.6 to 1.7 min on average (Table 2). Continuous singing lasted from a few minutes to over 40 min.

### Introductory mimicry

A 5-10 s standardised pattern of introductory mimicry,

common to all Winburndale Lyrebirds from Eskdale Gulf (location 3) to the Turon River, extended over a distance of at least 30 km. It was invariably a prelude to the territorial song. This mimicry used food begging calls of young Australian Magpie (or alternatively a similar-sounding Laughing Kookaburra laugh-prelude), honeyeater *chop* calls, Red Wattlebird calls and Grey Shrike-thrush song phrases. At locations 1, 2 and 3 this introductory mimicry could be considered as part of the song, while at location 4, and at another location near the Turon River, the sequence was a little more variable.

Songs from locations 6 and 7 had no pattern of introductory mimicry but location 5 songs were often preceded by a phrase of Grey Shrike-thrush mimicry. At locations 6 and 7, Grey Shrike-thrush calls were rarely used anywhere in the repertoire.

Other mimicry in the repertoire at all locations appeared to be at random. The introductory mimicry and the territorial songs from all locations are fully described in the captions of the figures.

## Discussion

This study of Superb Lyrebird territorial song in the Central Tablelands of New South Wales has seven main findings: (1) calling lyrebirds were not evenly distributed throughout native forest areas, but occurred in groups; (2) locationally distinct territorial songs were shared by all individuals within each group; (3) regional song variation occurred between groups; (4) song groups were in fixed locations; (5) multiple song use was fixed into the repertoire of some groups; (6) a standardised sequence of introductory mimicry was incorporated into some songs; and (7) songs remained constant over a period of time.

These findings support the belief that territorial song unites populations of closely related Superb Lyrebirds, and that such populations are not normally migratory.

Given that Superb Lyrebird populations can be identified by song, these groups could be further monitored to follow any displacement due to fire or other habitat disturbance. Further research is also required, over a longer period of time, to follow song evolution.

It is not yet understood how genetic diversity is maintained in apparently exclusive song groups. The songs indicate that interaction between neighbouring populations may be more widespread in the sandstone country than in the Winburndale Ranges. A similar territorial song occurs over a wider area, and population

groups are larger, in the sandstone country. However, the standardised sequence of introductory mimicry found in the smaller Winburndale populations indicates contact of birds over a wider area than the locationally distinct songs might suggest.

Geographical conditions may relate to song diversity, and Winburndale Superb Lyrebirds, at the westernmost limit of their range, may live in a more marginal habitat with hard and stoney soils (more difficult to rake through for feeding) and with altitude exposure to winter gales. Winburndale populations therefore breed and display only in the sheltered gullies, close to water and richer soils. These gullies are acoustically isolated due to steep and curving terrain, so that small populations are both physically and acoustically separated from one another. This may account for the greater variety of regional song types within the Winburndale Ranges. In the horizontally layered landscape of the sandstone locations, songs may carry further and populations may be partly continuous in the more widely suitable habitat, thus showing less variation in song types.

It might further be suggested that multiple song use in the Winburndale groups may have evolved after a compression of Superb Lyrebird populations caused by environmental pressures in the 1960s and 1970s when adjoining native forests were clear-felled. While this may be so, it does not hold true for location 1 nor for several other un-numbered Winburndale groups, which all had only one song type but were under equal pressures from clear-felling. Conversely, at Mt. Airly (location 5), the sandstone habitat is relatively undisturbed yet two songs were in evidence. No conclusion can be reached as to why multiple songs are used by any one group, although it does seem to indicate some contact between groups or individuals. It may well be that song learning in Superb Lyrebirds is more flexible than pre-

viously thought, with adult males able to adopt and combine new songs if forced into new territory.

While it can be shown that the Superb Lyrebird as a species is not endangered, small groups clearly are at risk and greater value should be put on their unique songs that are no less worthy of preservation than is the lyrebird itself.

It would be of considerable scientific value to produce a song-map of lyrebird populations over their entire range, so that the significance of regional variation in territorial songs can be fully evaluated.

## Acknowledgements

I would like to thank H. Sydney Curtis for making the audiograms, and Peter Fullagar, Darryl Jones, F. Norman Robinson, Ron Wooller, H. Sydney Curtis and Anonymous for commenting on the manuscript.

## References

- Bell, K. 1976. Song of the Superb Lyrebird in southeastern NSW, with some observations on habitat. *Emu* 76, 59-63
- Blakers, M., Davies, S.J.J.F. & Reilly, P.N. 1984. *The Atlas of Australian Birds*. RAOU and Melbourne University Press.
- Reilly, P. 1988. *The Lyrebird, A Natural History*. NSW University Press.
- Robinson, F.N. 1974. The function of vocal mimicry in some avian displays. *Emu* 74, 9-10.
- Robinson, F.N. 1975. Vocal mimicry and the evolution of bird song. *Emu* 75, 23-27.
- Robinson, F.N. & Curtis, H.S. 1996. Vocal displays of the Lyrebirds, Menuridae. *Emu*, in press.
- Taylor, I. 1986. The song of the Superb Lyrebird in the ACT. *Corella* 10, 46-54.
- Wall, L.E. & Wheeler, W.R. 1966. Lyrebirds in Tasmania. *Emu* 66, 123-131.