

A sonographic analysis of a flute-like dialect in territorial songs of the Superb Lyrebird *Menura novaehollandiae* in the New South Wales North Coast and New England Tableland Bioregions

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This paper examines flute-like territorial songs and other vocalisations of Superb Lyrebirds *Menura novaehollandiae* in forests of the New South Wales North Coast and New England Tableland Bioregions, based on >90 hours of recordings made from 1970 to 2014. Songs from a 1920s flute-mimicking lyrebird allegedly spread outwards from a fixed point at Allans Water. We examine potential evidence for this in territorial song structure, mimicry, and invitation-display calls across the region. In a macro-geographic overview, sonograms are paired with maps to establish spatial and temporal patterns of vocalisations, supplemented by audio links and transparent sonogram overlays. Distinctive and linked phrases of mimicry are used as markers to track temporal and spatial stability in song. Results indicate that the Superb Lyrebird's vocal repertoire in this area is stable, making it unlikely that a 'new song' was taken up quickly, as suggested in the 'flute' story. This finding corresponds with what is known of Superb Lyrebirds in other areas, namely that calls are learned mainly from conspecifics, show regional variation, and remain relatively consistent over time.

INTRODUCTION

Folklore suggests that songs from a 1920s flute-mimicking Superb Lyrebird spread outwards from the bird's release point at Allans Water, New South Wales (NSW) as the result of cultural transmission by male lyrebirds. Powys *et al.* (2013) and Taylor *et al.* (2019) recently investigated this phenomenon. They found that historical accounts were conflicted and could not confirm the source of these flute-like songs (hereinafter flute songs) (Powys *et al.* 2013). Recordings made in 2009-2014 documented the extent of the flute-like dialect, whilst ground searches and satellite imagery confirmed that forest habitat was continuous within the study area. Flute songs extended over a greater distance than previously thought (130 km) and could be easily distinguished from non-flute songs in the field (Taylor *et al.* 2019). Non-flute songs typically have steep frequency 'sweeps' that carry well over distance, whilst flute songs have short, discrete, flute-like notes of a type that may more easily degrade with distance (Richards 1981; Catchpole and Slater 2008).

Like many other songbirds, young lyrebird males learn to produce species-typical song by listening to nearby conspecific adult males. As a consequence of such vocal learning, song varies geographically within many avian species (Handley and Nelson 2005). When neighbouring birds have songs that are more similar than those of more distant birds, this is identified as a song dialect (Baptista and King, 1980; Krebs and Kroodsma 1980; MacDougall-Shackleton and MacDougall-Shackleton 2001). Vocal dialects are common (especially in sedentary populations) and taxonomically widespread, and have been documented in most songbirds that have been studied (Mundinger 1982; Kroodsma 2004). Song dialects are usually identified by researchers through subjective comparisons of sonograms (Baker and Cunningham 1985; Handley and Nelson 2005).

Dialect boundaries may or may not be clearly delineated (Krebs and Kroodsma 1980). Although dialects can be temporally stable (Mundinger 1982), they may change as a gradual cline, or rapidly and suddenly (Krebs and Kroodsma 1980). Dialect stability and longevity may depend on whether the species is sedentary or migratory, its lifespan, the security and continuity of its habitat, and whether the sensitive phase for song learning is open-ended. The causes and consequences of songbird dialects, including copy error (Slater *et al.* 1980), are longstanding problems in ornithology, with no single theory yet providing a full and convincing account of their origin and maintenance (Lemon 1975; Baker and Cunningham 1985; MacDougall-Shackleton and MacDougall-Shackleton 2001). The function of dialects, if there is one, remains contentious (Baker and Cunningham 1985).

Superb Lyrebirds are weak fliers and sedentary. Males and females have different habitat requirements for nesting and foraging (Maisey *et al.* 2019), but together they form aggregations in suitable habitat and are not evenly dispersed. A song dialect and other vocalisations are typically shared by clusters of breeding males that sing competitively to attract females. Males in hearing distance of one another all sing the same repertoire. Young lyrebirds mostly learn mimicry and other vocalisations from adult males rather than from mimicked models (Robinson and Curtis 1996). Longitudinal studies indicate that regionally distinct 'territorial songs' (Bell 1976; Robinson 1974; Powys 1995; Robinson and Curtis 1996; Proberts 2010; Taylor 2016) and mimicry show little change for up to 44 years (Higgins *et al.* 2001; Powys 1995, 2006).

The only other lyrebird, Albert's Lyrebird *Menura alberti*, has a repeating, sequential pattern of mimicry that varies regionally (Robinson and Curtis 1996). Most authors agree

that Superb Lyrebird mimicry occurs in a random order (Higgins *et al.* 2001). However, in a comparison of Superb Lyrebird mimicry in NSW between Yarramalong Valley, Royal National Park, and Blue Mountains National Park, Thorburn (1979) found that males sometimes had ‘favourite pairings’ of mimicked species. Zann and Dunstan (2008) found that Yellow-tailed Black-Cockatoo *Calyptorhynchus funereus* mimicry usually preceded territorial songs at both Kinglake and Sherbrooke Forest in Victoria, locations 40-50 km apart. Powys (1996) found territorial songs across 30 km in the Winburndale Ranges (Central Tablelands of NSW) to be preceded by a 5-10 sec. standardised pattern of introductory mimicry.

The present study builds on historical accounts and mapping, and examines evidence that bears on the likelihood of the flute story concerning lyrebird vocalisations in the forests of the NSW North Coast and New England Tableland Bioregions being correct. It examines song structure, mimicry, and ‘invitation-display calls’ (Kenyon 1972; Smith 1988, p. 33; Higgins *et al.* 2001, p. 154; Powys 2008) across this entire area.

Given that Superb Lyrebirds have stable vocal dialects and are sedentary, and that structurally the flute song may not transmit well through forest, earlier researchers have questioned the credibility of a mimicked flute tune from a once-tame lyrebird spreading ‘like wildfire’ through the landscape over 130 km (Rankin *et al.* 1999). Since this claim runs counter to what is known about lyrebirds, our study addresses the following questions:

1. How consistent are Superb Lyrebird songs, mimicry, and other calls temporally at any one location?
2. Do flute songs grade from complex to simple with distance from Allans Water (e.g. if a song spreads rapidly rather than slowly, might it become simplified or be incompletely learned)?
3. Do ‘flutist’ and ‘non-flutist’ males have any vocalisations in common?
4. Is there evidence of locationally-distinct mimicry, such as ‘favourite pairings of mimicked species’?
5. Is there evidence of the supposedly mimicked flute tunes, *Mosquito Dance* and *Keel Row*, in lyrebird songs?

METHODS

Study area

Fieldwork was conducted in the forests of the NSW North Coast Bioregion and the New England Tableland Bioregion across an area of approximately 200 km from north to south. Vegetation in the study area consisted of both *Eucalyptus* forest and rainforest, including Antarctic Beech *Nothofagus moorei* (Taylor *et al.* 2019). Clouds Creek State Forest was the northern-most survey site, Woko National Park the southern-most, Never Never Picnic Area (Dorrigo National Park) the most easterly site and Sheba Dam (between Nundle and Hanging Rock) the most westerly site. Of the 85 productive recording sites visited in nine field-survey trips, 37 were catalogued as ‘flute’ and 48 as ‘non-flute’ (Taylor *et al.* 2019). In Appendix 1 (and as tabled in Taylor *et al.* 2019), site location numbers correspond with GPS coordinates.

Sound recordings of lyrebird vocalisations

More than 58 hours of sound recordings were made from 2009-2014 using Olympus LS-10 Linear PCM Field Recorders and Sennheiser ME66 and ME67 shotgun microphones, and GPS locations of all recordings were noted. Recordings were made from 192 to 1,557m above sea level, and flute songs were found at elevations of 418 to 1,557m above sea level (Taylor *et al.* 2019). Recordings varied in duration. Efforts were made to record song for at least 30 min (and up to 86 min, mean duration 43 min) at sites not yielding flute songs, or to return to re-sample the site on another trip. Over 32 hours of archival recordings made by other researchers (extending from the 1970s to the early 1990s) were collated. Abbreviations for the recordists throughout the text are: SC=Syd Curtis, CP=Carol Proberts, ES=Ederic Slater, NF=Neville Fenton, HT=Hollis Taylor and JPU=Jane and Phillip Ulman. ‘AUDIO LINK’ indicates that an online audio file is available at http://caperteebirder.com/?page_id=1484 and subsequent pages, with some at quarter-speed to enhance their evaluation.

All 90+ hours of recordings were viable for analysis. Some recordings featured strong bouts of song and mimicry, whilst others had only partial songs or hints of songs, and sometimes very little mimicry. Some archival reel-to-reel and cassette recordings were discontinuous due to the recordist using the pause button and thus breaking up the patterns of mimicry. Recordings made at a distance or noisy recordings could not accurately reproduce mimicked species or song detail. No special attempt was made to record invitation-display calls, so the study of these is opportunistic, depending on what recordings were available.

Analyses

The 90+ hours of recent and archival recordings were collated, transcribed, and assessed by ear. ‘Twang’, ‘scale’, and territorial song notes in selected sequences were measured as notes per second by editing out other vocalisations, with the notes being counted aurally or visually from an expanded sonogram. Mimicry phrases were assessed from hand-written transcriptions, visually from sonograms, and aurally from the recordings. Territorial songs were compared visually using transparent overlays of sonograms in a graphics editor. Audio processing software included Sound Studio 4 (c2010-2017 Felt Tip Inc.). Sonograms were made using Amadeus Pro v2.5.3 (c1998-2017 HairerSoft) and processed using Adobe Photoshop Elements and an iMac computer with OS Mojave 10.14.3. Sonograms paired with maps summarise the findings, supported by supplemental audio files. Repertoires (including territorial songs, mimicry, and invitation-display calls) were scanned for locationally-specific vocalisations. Recent and archival recordings were compared. All sonograms presented are accompanied by online audio files.

RESULTS

Macro-geographic variation in flute territorial songs recorded from 2009-2014 at 11 locations

Macro-geographic variation in flute territorial songs was found across the study area, with a mix of songs from simple to more complex being observed (sonograms in Fig. 1 show both types). Simple songs contain notes that follow a single,

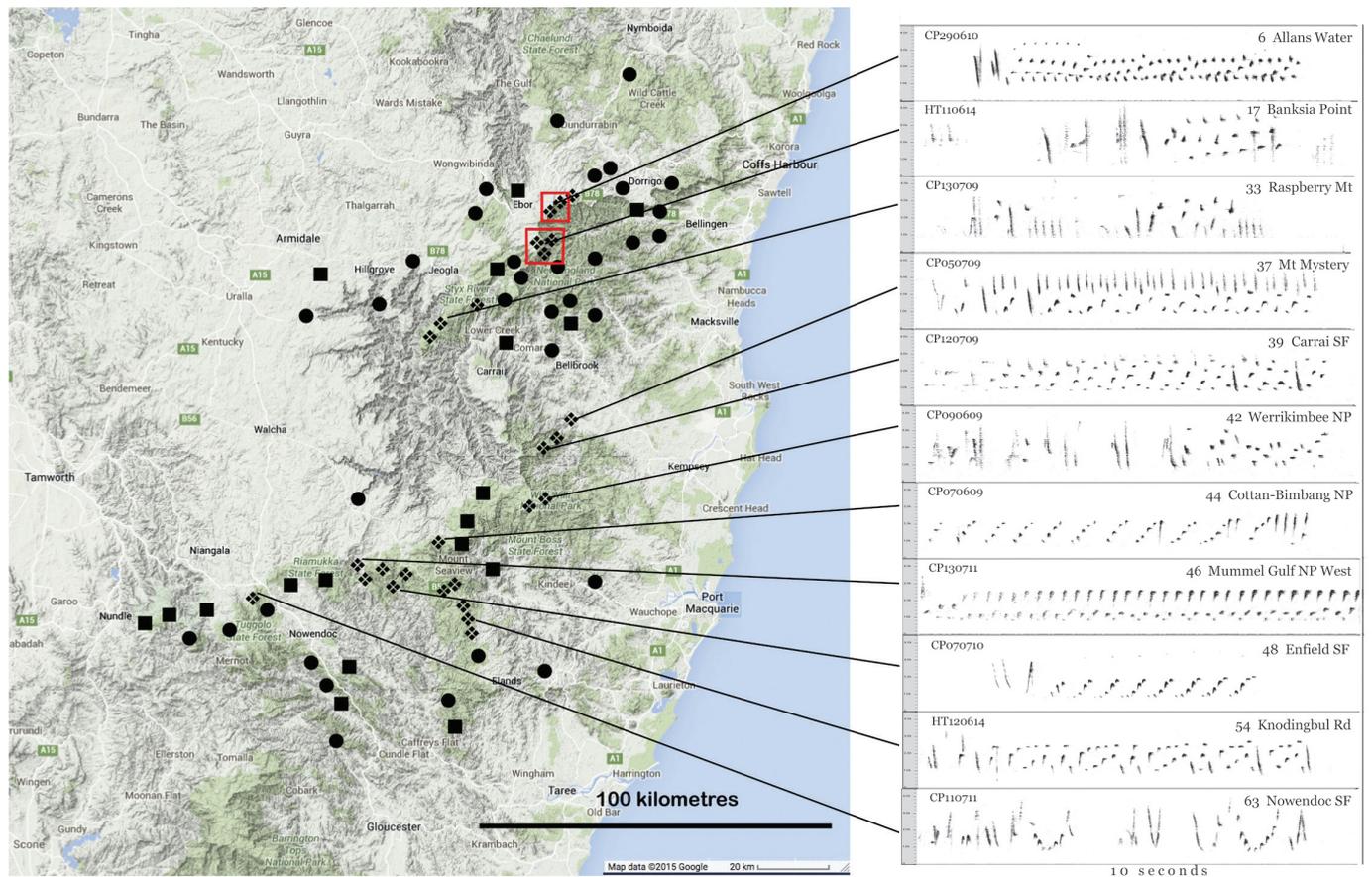


Figure 1. Macro-geographic variation in territorial songs 2009-2014, showing a variety of flute-song dialects across the study area. Recording sites are paired with a selection of 11 sonograms. ♦ = flute; ● = non-flute; ■ = no songs heard/recorded. Allans Water (top red box) is the site of the ‘original flute bird’ (see also Fig. 5.) Recordists’ initials and date are shown (day-month-year), as well as site number and name. AUDIO LINK is available at http://caperteebirder.com/?page_id=1484.

ascending line, such as those at sites 44 (Cottan-Bimbang National Park) and 48 (Enfield State Forest). Both these sites feature a repeated series of rising 4- and 5-note motifs that the human ear can easily follow in real time.

In more complex flute songs, the sonogram displays two or three concurrent ascending lines (but never simultaneous notes). This complexity is more readily confirmed by ear when the sound is slowed to half- or quarter-speed. For instance, at site 54 (Knodingbul Road), an alternating pair of low and high notes gradually rises, then the cycle returns to the lowest point and begins again. Increasing in complexity, Site 6 (Allans Water) has a three-ascending-line structure.

Table 1 presents measurements of the ‘dot’ note sections from five of the 10-second sonograms in Figure 1. Allans Water and Carrai had the fastest note rates, whereas Enfield had the narrowest range of notes and the lowest pitch.

Sonogram overlays in the supplementary files (ONLINE LINK: http://caperteebirder.com/?page_id=1474) show in more detail the structural similarities in flute songs from five locations across the study area. Where song patterns are similar, slight timing differences can produce misalignment in some notes, but in our analysis pattern matching took precedence over tempo. We contend that the degree of pattern likeness is clear from visual inspection. Included in the comparison are two

Table 1

Flute notes per second and range in kilohertz (kHz) for five locations from north to south, summarising the Figure 1 sonograms.

Location	Date: recordist	km from Allans Water	Notes per second	Range (kHz)
Allans Water	29/06/2010: CP	0	13	1.1 - 2.6
Carrai	12/07/2009: CP	68	10	0.8 - 2.6
Cottan-Bimbang	07/06/2009: CP	105	7	0.8 - 2.6
Enfield	07/07/2010: CP	120	8	0.7 - 2.0
Knodingbul	12/06/2014: HT	130	8	0.9 - 2.7

‘simple’ and three ‘complex’ songs. Allans Water, Carrai, and Knodingbul had some strong similarities and a complex note pattern, whilst Enfield and Cottan-Bimbang had a less complex note pattern and fewer notes. Additionally, online sonogram overlays of Allans Water songs compare: a) the same date and same bird (showing almost an exact match of notes), b) the same date, but a different bird 800m distant (showing a very close match), and c) the same location on different dates, 1981 and 2010 (showing a close match). They also reveal that song pattern differences were greater as a function of distance than over time (up to 44 years) at this location.

Historical comparison of flute songs at three locations

1. Allans Water

NF recorded at this site in July 1970, 50 years after the supposed release of the ‘original flute bird’ circa 1920. SC made recordings at this site in 1981, and ES recorded lyrebird songs 1 or 2 km farther east near Barren Mountain in 1988. Recordings by CP in 2010 and HT in 2014 were made near the locations at which FN and SC recorded. Territorial songs at Allans Water show similarities over 44 years (Figs. 2 and 2.1). Short, flute-like ‘dot’ notes (0.05 sec. duration) between 1-3 kHz in frequency occur at 10-12 notes per second, in gradually rising series of triplets and quadruplets. A transparent overlay of two sonograms from 1970 and 2010 (Fig. 2.1) reveals a remarkably similar note pattern. Several downward-sweeping, introductory notes are followed by several seconds of ‘dot’ notes that appear visually as a ‘rope-twist’ pattern. The small differences are minimal compared to geographic variation at other locations. The pattern of notes is also detailed in the *Song motifs* section below.

ALLANS WATER

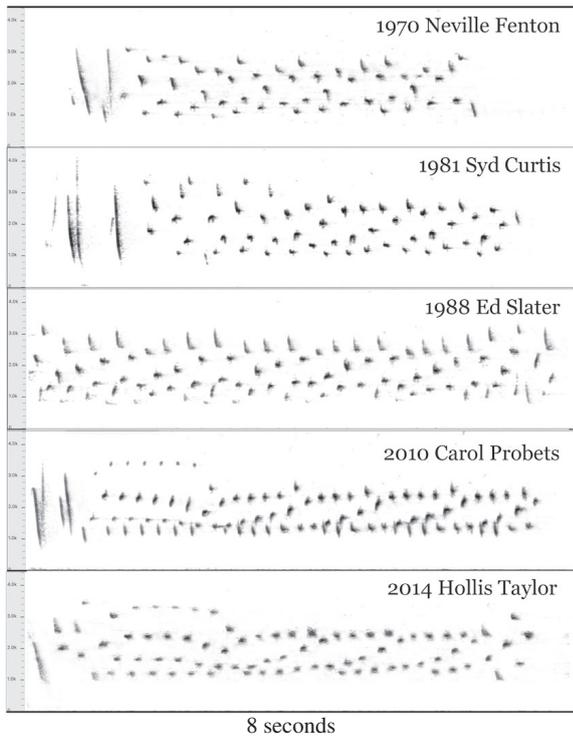


Figure 2. Sonograms of recordings made at Allans Water, 1970-2014. AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

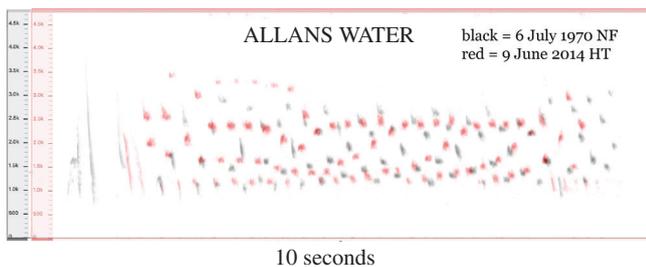


Figure 2.1. A transparent overlay of two sonograms showing similarities between 1970 (black) and 2014 (red) at Allans Water.

2. Carrai State Forest

Slater’s recordings from Carrai State Forest in June 1991 are consistent with those of CP, who visited the area in 2009 and 2010 (Fig. 3). It is unknown exactly where Slater recorded at Carrai, but it is likely to have been close to our sites 37 (Mt Mystery) and 39 (Kookaburra Camp, Carrai State Forest), which also feature in Figure 1. We contend that territorial songs in the Carrai area show similarities over 19 years, which are evident in more detail in Figure 6. ‘Dot’ notes are 0.05 sec. in duration, with 9-10 notes per second, and range in frequency from 0.8 to 3.1 kHz. The highest notes are streaky ‘chip’ sounds. The pattern of notes is detailed in the *Song Motifs* section below.

CARRAI

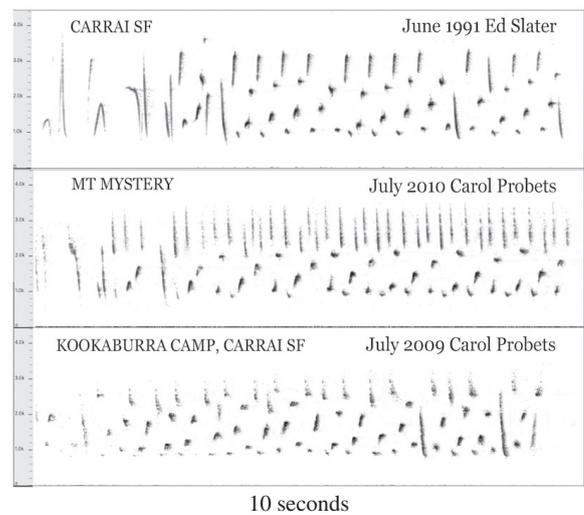


Figure 3. Sonograms of recordings made in the Carrai area, 1991-2010 (see also Fig. 6.) AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

3. Mt Boss

ES recorded at Cedar Road in Mt Boss State Forest in 1989, and at “Mt Boss” in 1991, with the exact location being unknown. CP visited nearby areas in 2009, namely sites 40 (Hastings Forest Way in Willi Willi National Park) and 42 (Plateau Beech camp, Werrikimbe National Park), which is shown in Figure 1). CP’s locations were 5.45 km apart, and 5-8 km from Cedar Road. Territorial songs from the Mt Boss area show apparent similarities over 20 years (Fig. 4) i.e. introductory notes are followed by ‘dot’ notes 0.05 sec. long and some short streaky notes, both delivered at 7-9 notes per second and ranging in frequency from 0.8 to 2.6 kHz. The pattern of notes is detailed in the *Song Motifs* section below.

Analysis of flute song motifs at three locations

Flute songs were examined at quarter-speed and divided into subsections (‘motifs’), which were found to be structurally distinct for each locality.

1. Song motifs at Allans Water

Allans Water songs (Fig. 5) combine two different motifs, switching between triplets and quadruplets, and gradually rising in pitch. Their motifs appear to be similar over 44 years.

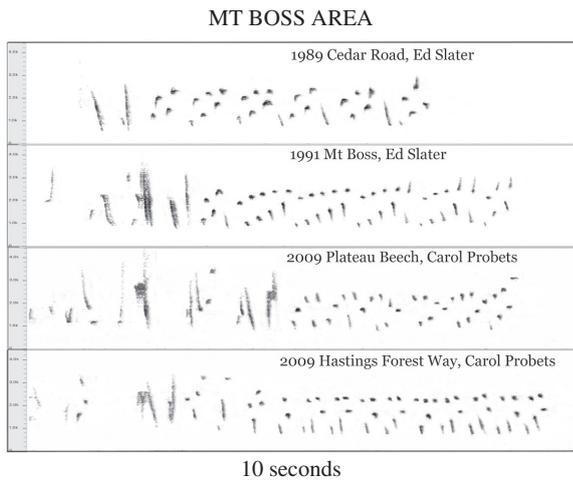


Figure 4. Sonograms of recordings made in the Mt Boss area, 1989-2009 (see also Fig. 7.) AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

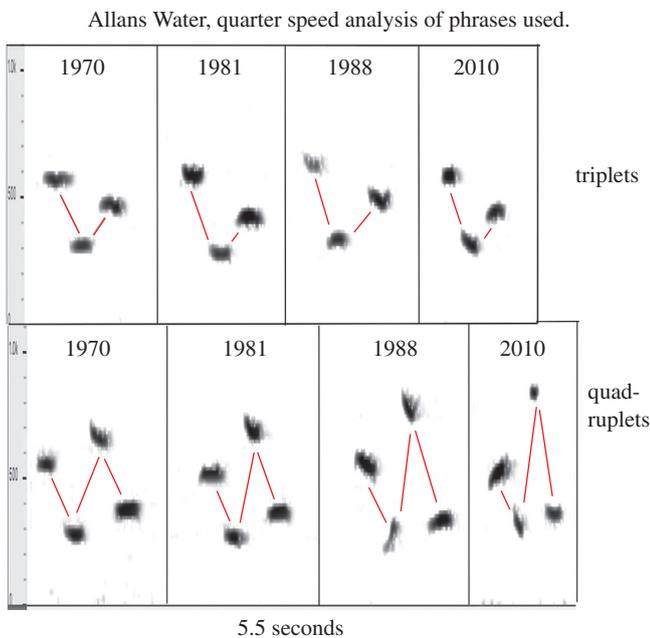


Figure 5. Triplets and quadruplets from Allans Water analysed from quarter-speed recordings. AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

2. Song motifs at Carrai State Forest

Carrai songs (Fig. 6) comprise a repeated quadruplet motif, with flute-like ‘dot’ notes and streaky ‘chip’ notes. The nearby Mt Mystery motif (recorded in 2010) begins and ends with a high streaky note, giving an effect like another bird twittering in the background. Motifs from the Carrai area (which includes sites 10 km apart) appear to be similar over 19 years; any small differences could be either geographic or temporal.

3. Song motifs at Mt Boss

A repeated, two-note motif was used in Mt Boss songs, ascending the scale and forming a zig-zag pattern of notes on the sonogram (Fig. 7). At Cedar Road in 1989, there were 2-3

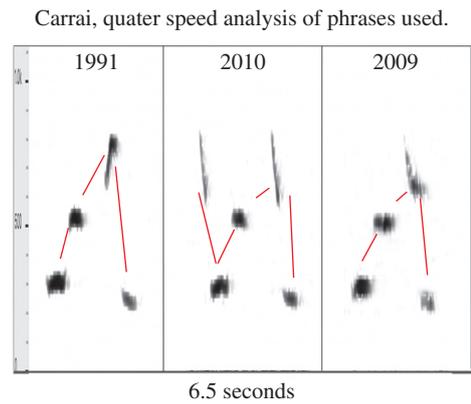


Figure 6. Song motifs from Carrai State Forest, analysed from quarter-speed recordings. AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

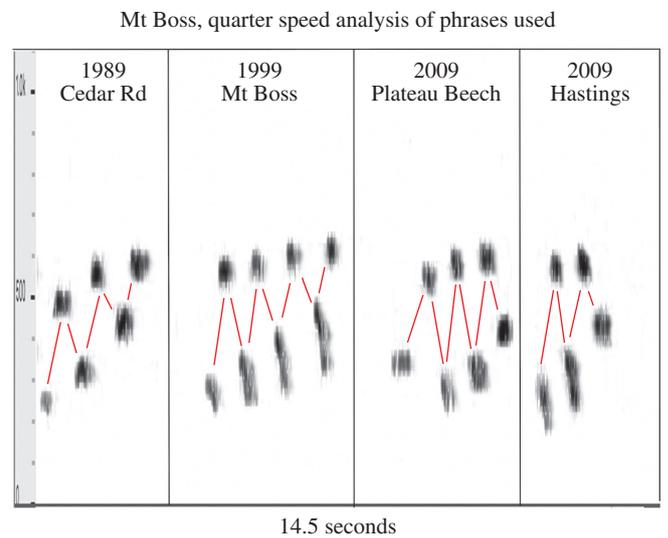


Figure 7. Song motifs from the Mt Boss area, analysed from quarter-speed recordings. AUDIO LINK is available at http://caperteebirder.com/?page_id=1504.

sets of rising doublets per phrase, most phrases ending with a descending note and a short pause. At Mt Boss in 1991 (exact location not known), there were 2-5 sets of rising doublets per phrase and no descending note or pause. Plateau Beech in 2009 had 3-5 doublets per phrase and Hastings Forest Way in 2009 2-5 doublets per phrase. Motifs from the Mt Boss area appear similar over 20 years; any small differences could be either geographic or temporal.

Macro-geographic comparison of an ascending scale at eight locations

The ‘original flute bird’ at Allans Water supposedly mimicked a flute player practising a chromatic (or rising semitone) scale, as well as two distinct tunes. Chromatic scales can be heard in early Allans Water recordings by SC (1970s and 1981) and by NF (1970). However, no scales are heard in Slater’s June 1988 recordings at nearby Barren Mountain, nor in Allans Water recordings made by HT and CP in 2009-2014.

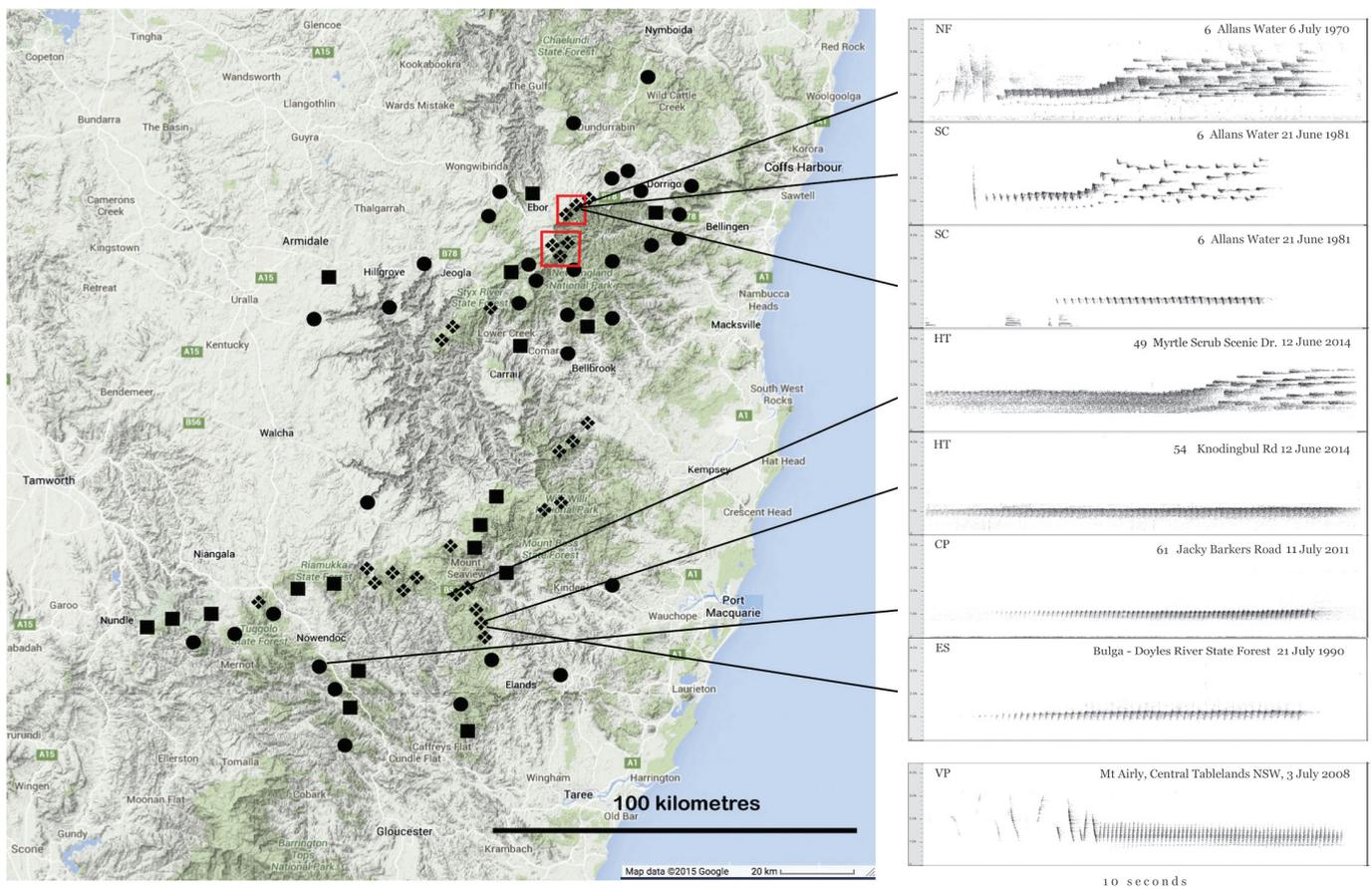


Figure 8. Seven scales from the study area, plus an eighth from Mt Airly in the Central Tablelands of NSW with a similar type of territorial song that is sometimes used as a stand-alone contact call. AUDIO LINK is available at http://caperteebirder.com/?page_id=1563.

Table 2

Measurements of scales.

Location	Date: recordist	Notes per second	Sample size (notes / seconds)	Description	Rising pitch range (kHz)
Allans Water	06/07/1970: NF	5.76	18 / 3.1	before ter. song	1.1 - 1.8
Allans Water	21/06/1981: SC	5.96	26 / 4.3	solo	1.2 - 1.3
Allans Water	21/06/1981: SC	5.86	17 / 2.9	before ter. song	1.3 - 2.2
Myrtle Scrub	12/06/2014: HT	7.54	43 / 5.7	before ter. song	1.6 - 2.1
Knodingbul Rd	12/06/2014: HT	6.9	60 / 8.6	solo	1.0 - 1.1
Jacky Barker Rd	11/07/2011: CP	9.8	49 / 5.0	solo	1.0 - 1.2
Bulga/Doyles Rd	21/07/1990: ES	6.68	47 / 7.0	solo	1.0 - 1.2
Mt Airly	03/07/2008: VP	10.5	42 / 4.0	part of ter. song	1.3 - 1.3

In other parts of our study area, scales occur south of the Oxley Highway, being heard alone or preceding a territorial song. The highway is not considered to be a barrier to lyrebird movement (Taylor *et al.* 2019). Figure 8 shows seven scales from our study area, and an eighth from Mt Airly in the Central Tablelands of NSW that occurs both as a territorial song and as a stand-alone contact call (e.g. the call can occur as a long trill of up to nine or more seconds, without mimicry or preliminary notes, given intermittently by males while foraging and typically being answered by other nearby males).

Scales preceding a territorial song rise more steeply than stand-alone scales and occurred at Allans Water in 1970 and 1981, and at Myrtle Scrub Scenic Drive (site 49), 120 km to the south, in 2014. A stand-alone scale occurred within a sequence of mimicry at Allans Water in 1981 (Fig. 8), with somewhat similar scales being observed at Bulga/Doyles River (1990), Knodingbul Road (2014) and Jacky Barkers Road (2011). Thus, scale-like vocalisations appear to be a normal part of the lyrebird repertoire in our study area and occur also outside of it.

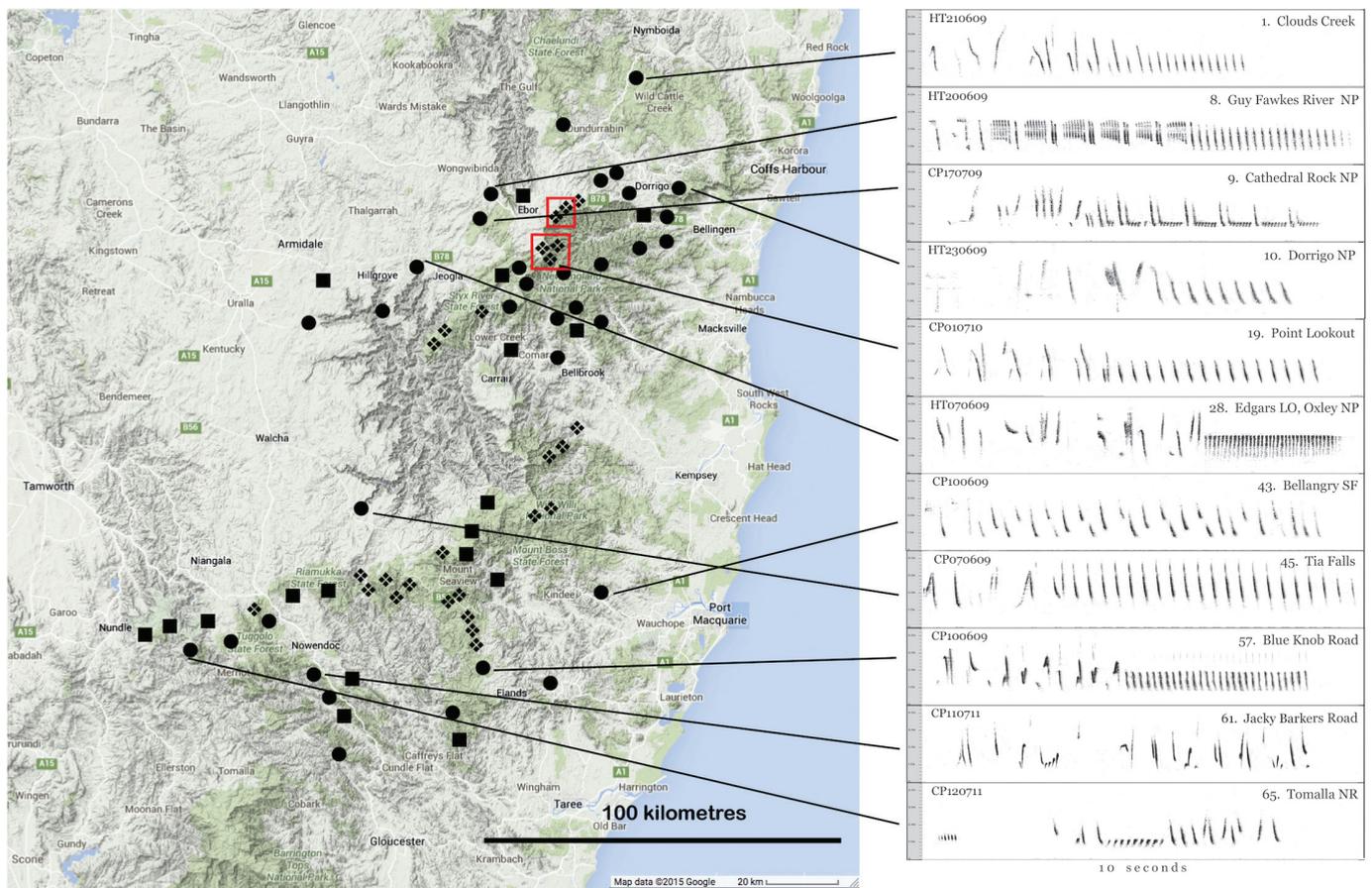


Figure 9. Variation of dialects in a selection of 11 non-flute territorial songs in our study area. AUDIO LINK is available at http://caperteebird.com/?page_id=1578.

Table 2 details measurements of these scales, with 5-6 notes per second at Allans Water, slightly faster delivery at four sites further south (6-10 notes), and 10 notes at Mt Airly. All stand-alone scales rose very slightly in pitch (0.1-0.2 kHz), except for those at Mt Airly, which had a consistent pitch. Scales preceding a territorial song rose more steeply (0.5-0.9 kHz).

Macro-geographic variation in non-flute territorial songs 2009-2014 at 11 locations

Considerable variation is found in the non-flute territorial songs in our study area (Fig. 9), the simplest version consisting of the repetition of a single, descending note (*chu-chu-chu*) e.g. sites 10 (Dorrigo National Park) and 19 (Point Lookout). Some Point Lookout individuals sang both flute and non-flute songs, whilst at Dorrigo National Park on multiple visits, no flute songs were heard. Sites 8 (Guy Fawkes River National Park) and 9 (Cathedral Rock National Park) had quite complex non-flute songs. At site 61 (Jacky Barkers Rd, 2011) in a recording lasting 12.16 minutes, there were five non-flute territorial songs (Fig. 9) and six slightly rising 'scales' (Fig. 8). The scale may have functioned as a second territorial song. As no archival recordings of non-flute songs were available for the period before 2009 for the study area, no historical comparison of non-flute songs could be made.

Mimicry at two locations 90 km apart

We do not attempt here to describe every mimicked call at Allans Water and Mt Boss; only the variants that were most

obvious, including favourite pairings, are summarised. Suites of mimicry from Allans Water recorded from 1973-2010 were compared geographically and temporally with mimicry from the Mt Boss area recorded from 1991-2009. Whilst the arrays of bird species mimicked were similar at these two localities, the phrases selected by lyrebirds and how they are combined in their mimicry were unique to each locality.

- (a) Bird species mimicked at both locations: Grey Shrike-thrush *Colluricincla harmonica*, Crimson Rosella *Platycercus elegans*, Pied Currawong *Strepera graculina*, Satin Bowerbird *Ptilonorhynchus violaceus*, Laughing Kookaburra *Dacelo novaeguineae*, Eastern Whipbird *Psophodes olivaceus* and Yellow-tailed Black-Cockatoo *Calyptorhynchus funereus*.
- (b) Bird species mimicked only at Allans Water: King Parrot *Alisterus scapularis*.
- (c) Bird species mimicked only at Mt Boss: Glossy Black-Cockatoo *Calyptorhynchus lathami*, Green Catbird *Ailuroedus crassirostris* and Australian Logrunner *Orthonyx temminckii*.
- (d) Distinctive phrases and linked phrases: At Allans Water for all years considered, a distinct Pied Currawong call was often used (Fig. 10). Two phrases were often linked - a Crimson Rosella call was immediately followed by a Grey Shrike-thrush call (Table 3, Fig. 11). The Crimson Rosella

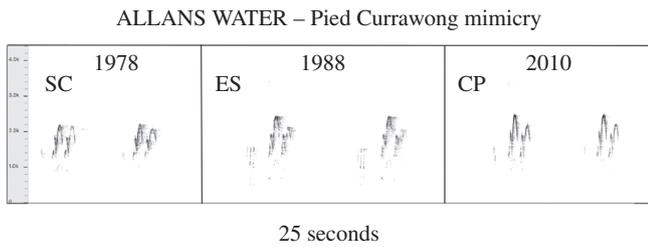


Figure 10. Two examples of Pied Currawong mimicry from 1978, 1988, and 2010 at Allans Water (*curra-WAH curra-WAH*). This phrase did not occur at Mt Boss. AUDIO LINK is available at http://caperteebirder.com/?page_id=1596.

ALLANS WATER – Crimson Rosella & Grey Shrike-thrush mimicry

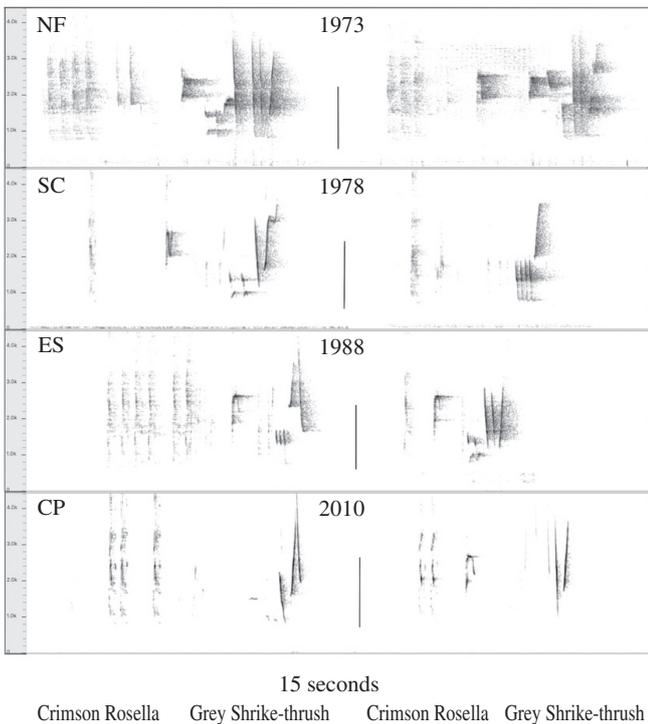


Figure 11. Two examples of linked Crimson Rosella and Grey Shrike-thrush mimicry from each of the years 1973, 1978, 1988, and 2010 at Allans Water. AUDIO LINK is available at http://caperteebirder.com/?page_id=1596.

calls included 1-3 types (flight, bell, and chatter calls), and the Grey Shrike-thrush calls also included 1-3 types (1-note, rattle, and melody calls). Territorial songs were usually preceded by a Satin Bowerbird call (Table 4, Fig. 12). These Satin Bowerbird calls included 1-3 types (whirr, wow, and harsh calls). None of these variants occurred at Mt Boss.

In 15.5 minutes of recording from one lyrebird at Mt Boss, territorial songs were very often preceded by a Yellow-tailed Black-Cockatoo call or a Glossy Black-Cockatoo call in both 1991 (77.7%) and 2009 (86.6%) (Table 5, Fig. 13). However, there were no obvious phrase linkages. Two main variations of a Pied Currawong call appeared similar for 1991 and 2009, but different from the Allans Water version (Fig. 14). Thus, over time, distinctive and linked phrases given at any one locality remained much the same.

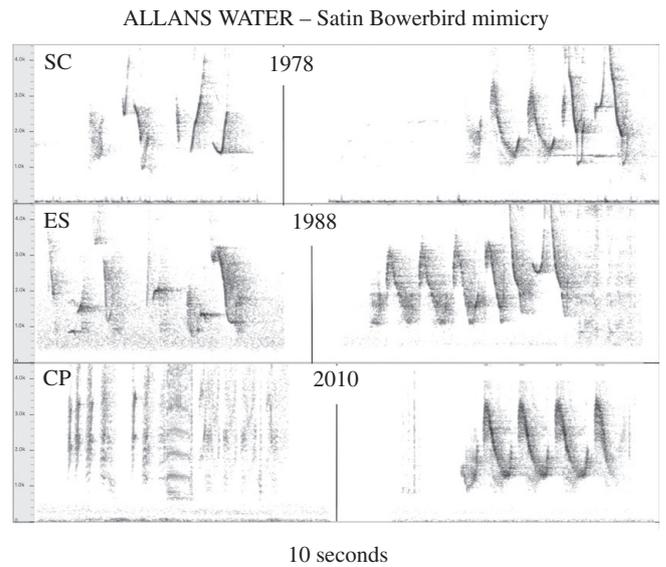


Figure 12. Two examples of Satin Bowerbird mimicry that preceded a territorial song from 1978, 1988, and 2010 at Allans Water. AUDIO LINK is available at http://caperteebirder.com/?page_id=1596.

Table 3

Linked phrases of Crimson Rosella (CR) at Allans Water. GST = Grey Shrike-thrush; EW = Eastern Whipbird.

Year	Duration (min) / recordist	CR calls	Linked with GST	Linked with EW
1978	17 / SC	14	9 (64%)	4 (28%)
1981	44 / SC	25	16 (64%)	7 (28%)
1988	47 / ES	40	10 (25%)	19 (47%)
2010	34 / CP	48	28 (58%)	12 (25%)

Table 4

Mimicked species that precede a territorial song at Allans Water. SBB = Satin Bowerbird.

Year	Duration (mins) / recordist	Total songs	SBB	Mixed species
1978	22 / SC	12	8 (66%)	4
1978	17 / SC	13	8 (61%)	5
1981	44 / SC	37	16 (43%)	21
1988	47 / ES	34	22 (64%)	12
2010	34 / CP	47	29 (61%)	18

Variation in invitation-display calls from five locations

Invitation-display calls, including twanging, thudding (*pluggerah*) and loud *blick* calls, are given by displaying male Superb Lyrebirds and exhibit regional variations in pattern across their range (Powys 2008). Locationally-distinct, rhythmic patterns occurred within the study area. Figure 15 and Table 6 showed similarities over time at Allans Water (1988 and 2009), with similar calls being used at nearby Banksia Point in 2010; Mt Boss, Myrtle Scrub, and Enfield State Forest, which are farther away, showed geographical differences to one another and to Allans Water.

Table 5

Mimicked species that precede a territorial song at Mt Boss. Cockatoo = Yellow-tailed Black-Cockatoo and Glossy Black-Cockatoo, about 50% each.

Year	Duration (mins) / recordist	Total Songs	Cockatoo	Mixed species
1991	16 / ES	18	14 (77%)	4
2009	13 / CP	15	13 (86%)	2

MT BOSS area – Yellow-tailed and Glossy Black-Cockatoo mimicry

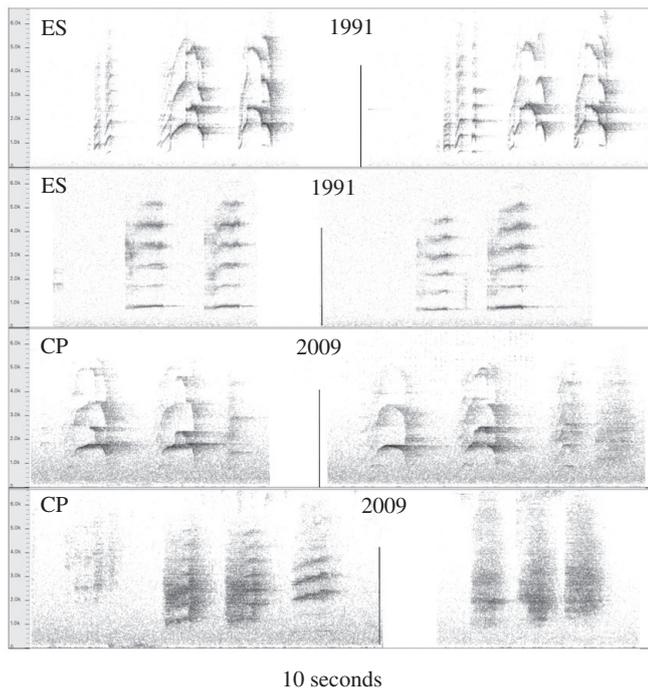


Figure 13. Two examples of Yellow-tailed Black-Cockatoo and Glossy Black-Cockatoo mimicry that preceded a territorial song, from 1991 and 2009, respectively, in the Mt Boss area. Note that in 2009, the Glossy Black-Cockatoo mimicry was minimal and replaced by a more general cockatoo sound. AUDIO LINK is available at http://caperteebirder.com/?page_id=1596.

Twanging calls were uttered at a faster tempo at Allans Water and Banksia Point than at the other three locations. Myrtle Scrub and Enfield had slower-tempo twangs delivered with regular pauses that suggest a rhythmic grouping (Table 6). The loud *klok* sound at Allans Water and Banksia Point is distinctive, sounding like a stick hitting a hollow tree. A similar sound occurred at Girraween (180 km north of Allans Water), but did not at Mt Boss, Myrtle Scrub, or Enfield. Mt Boss is 90 km south of Allans Water, whilst Myrtle Scrub and Enfield are 40-50 km south of Mt Boss and 15 km apart from each other.

This comparison of invitation-display calls is consistent with what is known for Superb Lyrebirds in other areas, and suggests that these calls are learned from other lyrebirds, show regional variation, and are temporally stable.

MT BOSS area – Pied Currawong mimicry

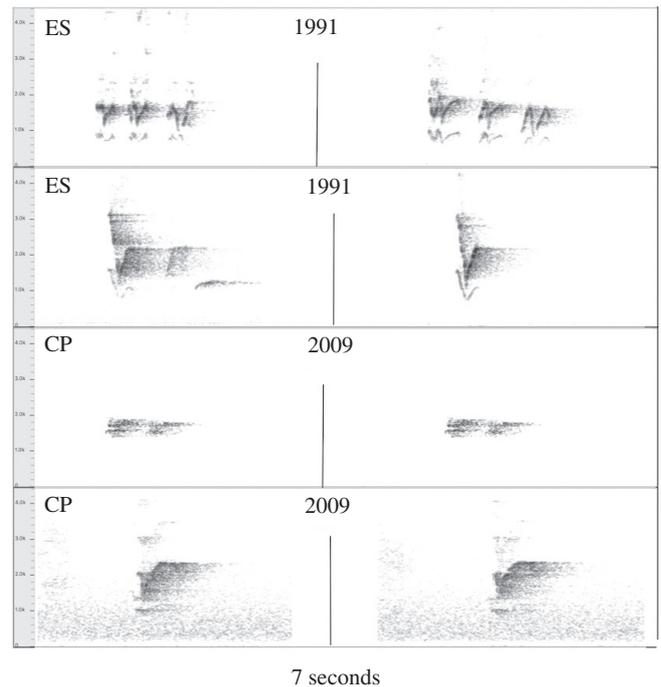


Figure 14. Examples of two different phrases of Pied Currawong mimicry from 1991 and 2009 in the Mt Boss area (rapid 'currawong-currawong-currawong' and 'kee-wah'). Note that these phrases were not used at Allans Water. AUDIO LINK is available at http://caperteebirder.com/?page_id=1596.

Vocalisations in common between flute and non-flute lyrebirds

A preliminary examination of vocal repertoire found similarities in patterns of mimicry between nearby localities. For example, at Johnsens Road near Dorriggo in 2014 (sites 72 and 73), a non-flute lyrebird usually preceded its territorial songs with Satin Bowerbird mimicry (4 out of 5 times), and gave linked phrases of a Crimson Rosella flight call immediately followed by a Grey Shrike-thrush call (3 examples in an 11-minute sequence). These patterns also occurred with flute lyrebirds at Allans Water 15-18 km to the west (Figs. 11 and 12, Tables 3 and 4). At Petroi Road, Lower Creek State Forest (sites 79, 80, and 81), a non-flute lyrebird preceded its territorial songs with Yellow-tailed Black-Cockatoo mimicry three out of four times, a sequence which also occurred with flute lyrebirds in the Mt Boss area 55 km to the south (Fig. 13, Table 5).

DISCUSSION

Relevance of cultural transmission of Tasmanian lyrebird vocalisations to the flute song phenomenon

Victorian Superb Lyrebirds were introduced to Tasmania between 1934 and 1949 (Higgins *et al.* 2001). Jordan (2007) visited Tasmania in 2006 and found that mimicry of the Eastern Whipbird and Satin Bowerbird had persisted for more than sixty years, even though these species do not occur in Tasmania. Meanwhile, Tasmanian endemic bird species had been added to the repertoire. Flute-like territorial songs in our study area may not be mimicry, but the Tasmanian findings indicate that

Table 6

Comparison of invitation-display calls. Dashes indicate a pause replacing a note, creating a rhythmic grouping.

Location / year	B = blink; T = twang; P = pluggerah	Twangs per sec. (n)
Allans Water / 1988 and 2009	B/TTTTTTTT/B/ alternating with BB/PP/klok/P	5.6 (n=112) and 4.8 (n=131)
Banksia Point / 2014	B/TTTTTTTT/B alternating with BB/PP/klok/P	4.1 (n=69)
Mt Boss / 1991	TTT and BB/PPP (short recording only)	not measureable
Myrtle Scrub / 2014	B/TTT-T/TTT-T-/ alternating with BB/PPP	2.9 (n=134)
Enfield SF / 2014	B/TTT-T/TTT-T-/ alternating with BB/PPP	2.7 (n=31)

INVITATION – DISPLAY CALLS

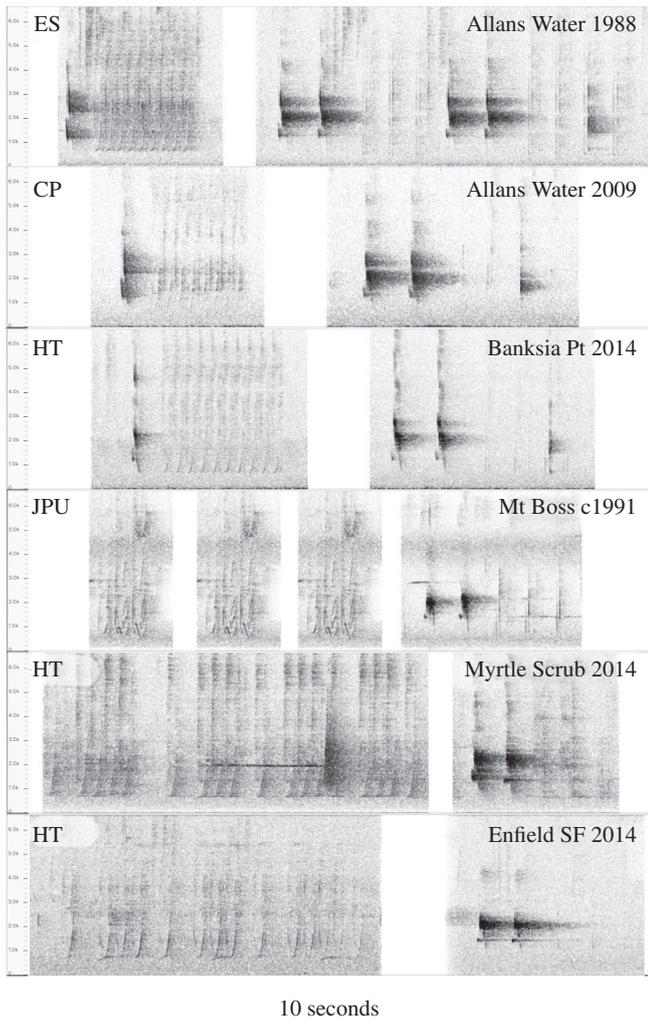


Figure 15. Invitation-display calls from Allans Water (1988 and 2009), Banksia Point (2014), Mt Boss (c.1991), Myrtle Scrub (2014), and Enfield State Forest (2014). Each year shows twanging calls, then blink-blick pluggerah calls. AUDIO LINK is available at http://caperteebirder.com/?page_id=1614.

Superb Lyrebirds’ capacity for vocal learning encompasses both the original models and other lyrebirds, which conforms with the findings of Putland *et al.* (2006). So, whilst the rapid uptake of a new model might be possible, a more likely scenario is a gradual, localised adoption of endemics’ vocalisations in multiple smaller areas (as the lyrebirds spread out), rather than

one individual (rapidly) influencing all the others to follow suit. Conversely, lyrebirds at Hastings in Tasmania have (for over 50 years) retained the territorial song of Toolangi, Victoria, from where they were transported in 1945 (Robinson and Curtis 1996). This makes it less likely that a new territorial song was taken up rapidly at Allans Water.

Cultural transmission of vocalisations in our study area

The longest recorded movement of a banded Superb Lyrebird is 10 km (Higgins *et al.* 2001), and they can live for 25 years (Reilly 1988). It is not known if, or how far, males or females move away from their natal area for breeding purposes. Taylor *et al.* (2019) found that continuous habitat occurred across our study area in the 1920-30s, with some habitat corridors remaining today, so theoretically long-distance cultural transmission of the flute song was possible. However, lyrebirds are sedentary, so the only way for the flute song to spread outwards from Allans Water would have been for the birds within earshot of a flute song individual to gradually take up these new sounds. Lyrebird song can be heard by humans up to one kilometre away, but given that the rapid notes of the flute songs degrade quickly due to attenuation and reverberation and thus lose their detail, it is unlikely that they could be learned accurately from distant birds singing from mountain tops. If songs were misheard at a distance (or incompletely learned), one might expect that they would become progressively simpler with distance from the ‘original bird’ supposedly released at Allans Water in the 1920s. However, we found that songs were complex at Allans Water and Carrai, simple in the central part of the study area (such as site 44 (Cottan-Bimbang National Park), but complex again south of the Oxley Highway near the southern boundary of our study area (as at site 54, Knodingbul Road). Given that songs were equally complex at both ends of the study area, this would seem to rule out a macro-geographic ‘complex-to-simple’ scenario of the kind that might be expected if males were learning the flute song from distant individuals.

The generally slow incorporation of new models into males’ suites of mimicry corroborated in our study also makes the possibility of a rapidly-spreading, novel song unlikely. Historically, flute-like territorial songs were consistent at Allans Water, with limited changes occurring over 44 years. At the Carrai and Mt Boss areas, no marked changes occurred in flute songs over 19 and 20 years, respectively.

Ascending scales were recorded at Allans Water 1970-1981, and one was also observed about 120 km to the south at site 49 (Myrtle Scrub Scenic Drive) by HT in 2014. At Mt Airly (Central Tablelands of NSW), the stand-alone scale (with the addition of preliminary notes) is also used as one of two

territorial songs (Powys, Taylor and Proberts, unpublished data). No scales were recorded at Allans Water by ES in 1988, nor by CP and HT in 2009–2014. The scale could have a specific function, but this remains unresolved.

Given that the suites of mimicry were stable for up to 37 years at Allans Water and Mt Boss, which are 90 km apart, our findings concur with those of other studies in suggesting that they develop slowly in any one area and are shared by all males at any one location (Thorburn 1979; Powys 1995, 2006 and 2008; Zann and Dunstan 2008).

One early proponent of the flute song story suggested that two songs were mimicked, namely *Keel Row* and *Mosquito Dance* (Powys *et al.* 2013). No evidence of the latter was found in flute lyrebird songs in our investigation. *Keel Row* does have a similar melodic contour (three ascending notes) to the Allans Water flute song. However, as lyrebirds are accurate and faithful mimics (Dalziell and Magrath 2012) and the released captive bird was purported to have sung *Keel Row* accurately, the question remains of why only a small trace of similar melodic contour remains. Further complicating this issue is the fact that the Allans Water flute song is long and complex, potentially making it much more difficult to learn than eight bars of *Keel Row*. Another difficult issue is that if the flute song was learned from a released bird, did the learners suddenly drop their existing song? As the ‘original’ territorial song is unknown, there seems to be no way of knowing if remnants of it persist.

In comparing flute and non-flute repertoires, our findings suggest that the flute repertoire only differs in the type of territorial song produced. In other aspects (suites of mimicry, invitation-display calls, and scales), flutists and non-flutists are virtually indistinguishable, which neither supports nor contradicts the flute song story. Some parts of the song repertoire were shared over a greater area than others; for example, the same ‘favourite’ mimicry phrases occurred in areas 18 km apart, but in populations where the territorial songs were totally different (being flute and non-flute). From this observation, it could be inferred that territorial song versions are more localized than mimicry.

Invitation-display calls have a rhythm that is synchronised with the male lyrebird’s dance on a display mound (Powys 2008; Dalziell *et al.* 2013). The most obvious movement is that of hopping or jumping, which occurs in time with a thudding call. Locationally-distinct rhythms suggest that there are different styles of dance in different areas. It may be that all the components of the Superb Lyrebird repertoire—territorial song, suites of mimicry, and invitation-display calls (plus dance style) are interlinked or co-dependent in some way, so that one aspect could not change quickly without affecting the others.

CONCLUSIONS

It is well known that dialects in the Superb Lyrebird’s territorial song occur throughout its range. Our study in the forests of the NSW North Coast and New England Tableland Bioregions additionally shows that although such variation occurs from location to location, territorial songs and other vocalisations have remained stable at certain locations for decades, based on recordings made from 1970–2014. These findings suggest that it is unlikely that a ‘new song’, the flute song, was introduced and taken up over a wide area since, say, 1920.

Although Allans Water flute songs are among the most complex in the study area, our evidence does not demonstrate this complex song becoming progressively simpler with increased distance from the ‘original flute bird’, as might be expected (due to attenuation and distortion) if males were learning it from other males some substantial distance away.

Our study found no reports of other flute-like songs across the entire geographical range of the Superb Lyrebird. This flute-like song type (with all its variations) seems to be restricted to northern NSW, but covers a large area more than 130 km from north to south. Vocal similarities between flute and non-flute lyrebirds within the study area included the sharing of mimicry patterns between nearby localities, indicating links between these populations. We did not test whether the distribution of flute songs reflects the genetic structure of lyrebird populations. It remains unknown why some birds sing both flute and non-flute songs, and why flute and non-flute song populations are intermixed across the study area.

This study confirms and expands findings by Thorburn (1979) and Zann and Dunstan (2008) regarding Superb Lyrebird mimicry. It provides the first evidence that (a) pairings of the vocalisations of mimicked species and (b) a specific mimicked call preceding a territorial song, can both be locationally-distinct and persist over time. These calls, plus other favourite mimicked phrases, can become reliable markers in studies of lyrebird vocal repertoire.

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Appendix 1

Recording sites mentioned in the text. Sites 1-65 are from N to S; 72-85 re-start from N to S. SF = State Forest, NP = National Park, and NENP = New England National Park.

Site	Location	Flute song	GPS South, East	Alt
1	Clouds Creek SF	no		
6	Allans Water forest, NENP	YES	30 23 19.4, 152 27 09.1	
8	Native Dog RA/Guy Fawkes River NP	no	30 23 14.7, 152 16 05.8	1,255
9	Cathedral Rock NP walking track	no	30 25 49.3, 152 15 03.7	1,481
10	Never Never picnic area, Dorrigo NP	no	30 21 28.1, 152 47 29.2	748
17	Banksia Point LO, NENP	YES	30 29 33.0, 152 24 23.6	1,446
19	Wrights LO, near Pt Lookout	YES	30 30 19.2, 152 23 50.9	1,322
28	Edgars LO, Oxley Wild Rivers NP	no	30 31 57.7, 152 01 34.3	1,018
33	Raspberry Mtn, Cedar Rd, Styx River SF	YES	30 42 40.0, 152 06 06.3	910
37	Mt Mystery Timber Reserve	YES	30 56 53.4, 152 24 18.1	418
39	Kookaburra Forest Camp, Carrai SF	YES	31 01 27.2, 152 20 13.8	960
40	Hastings Forest Way, Willi Willi NP	YES	31 09 38.8, 152 22 46.2	1,012
42	Plateau Beech camp, Werrikimbe NP	YES	31 10 48.2, 152 19 35.4	1,055

Appendix 1 (continued)

Recording sites mentioned in the text. Sites 1-65 are from N to S; 72-85 re-start from N to S. SF = State Forest, NP = National Park, and NENP = New England National Park.

Site	Location	Flute song	GPS South, East	Alt
43	No 1 Tower LO (Five Ways Hill), Bellangry SF	no	31 17 09.9, 152 32 08.3	661
44	Fenwicks Rd, Cottan-Bimbang NP	YES	31 16 32.6, 152 04 34.1	1,029
45	Tia Falls, Oxley Wild Rivers NP	no	31 09 23.2, 151 51 29.8	1,053
46	Mummel Gulf NP West	YES	31 19 07.1, 151 47 20.2	1,286
48	Mummel Gulf NP, Enfield Forest Rd	YES	31 21 04.6, 151 52 09.2	1,091
49	Myrtle Scrub Scenic Dr NW end, Cottan-Bimbang NP	YES	31 20 57.0, 152 00 52.9	1,154
54	Knodingbul Rd #1, Cottan-Bimbang NP	YES	31 28 06.5, 152 09 15.7	632
57	Knodingbul Rd/Blue Knob Rd junction, Bulga	no	31 34 41.4, 152 10 47.9	773
61	Jacky Barkers Road, Giro SF	no	31 33 22.0, 151 34 57.3	911
63	Myall Ck campsite, Nowendoc SF	YES	31 25 43.5, 151 33 27.2	914
65	Tomalla NR	no	31 31 53.6, 151 21 41.4	1,132
72	Johnsens Rd nr Dorrigo	no	30 20 20.0, 152 37 13.9	986
73	Johnsens Rd nr Dorrigo	no	30 20 20.0, 152 37 00.9	868
79	Lower Creek SF/ Petroi Rd	no	30 40 50.2, 152 14 53.9	417
80	Lower Creek SF/ Petroi Rd	no	30 40 01.8, 152 15 30.1	652
81	Lower Ck SF/ Petroi Rd ridge	no	30 39 42.9, 152 15 41.6	766
85	Woko NP/Cliff Track	no	31 47 45.2, 151 47 52.4	317
	Sheba Dam	N/A	31 29 57.3, 151 11 52.9	