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REGENT HONEYEATERS – MAPPING THEIR MOVEMENTS THROUGH SONG

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The endangered Regent Honeyeater *Anthochaera phrygia* once occurred over a wide range including South Australia, Victoria, Australian Capital Territory, New South Wales and Queensland, but now has only three core breeding sites: at Chiltern in Victoria, at Capertee Valley in New South Wales and west of Armidale in New South Wales. Breeding also occasionally takes place near Warwick in Queensland. Anecdotal evidence suggests that due to a population contraction Regent Honeyeaters may have formed three discrete populations each with its own dialect. This study investigates that proposal. An analysis of recorded song phrases 1977–2008 showed links between Chiltern, Capertee Valley and Armidale, and unexpectedly, that songs change over time at any one location. This paper compares and illustrates, with sonograms, the known main songs and calls of this species, including those of captive-bred birds. There have been no previous geographical comparisons of Regent Honeyeater vocalisations, very few sonograms have been published, and descriptions of calls in the literature are confusing. This study shows that there are stronger links between the three main population centres than colour banding has so far indicated.

INTRODUCTION

Vocalisations

Geographical and temporal variation in bird song have been described by many authors and are thought to indicate song learning in birds (e.g. Kroodsma and Baylis 1982; Catchpole and Slater 1995; Kroodsma 2005; Podos and Warren 2007). The terms "geographical variation" and "dialect" are used where localised populations have a shared vocabulary of song phrases that they copy from one another. With distance between populations, those song phrases become increasingly different. Copying errors combined with the active generation of new syllables and phrases can lead to variation over time (e.g. Andrew 1962; Lemon 1975; Bitterbaum and Baptista 1979; Wiens 1982; Morton 1987; Brown *et al.* 1988; Farabaugh *et al.* 1988).

I propose that if song learning and geographical variation in song can be demonstrated in the Regent Honeyeater, similarities of song phrases between geographically distant populations may show an interchange of birds between those locations.

There are few studies that track the movements of a nomadic bird through an analysis of its songs. In one example, the nomadic Red Crossbill *Loxia curvirostra* of North America had different vocalisations between eight subspecies which enabled tracking of those subspecies (e.g. Groth 1993; Young 2008).

Vocalisations of the majority of Australia's 71 species of honeyeater have been poorly studied (Higgins *et al.* 2001). Geographical variation has been described for nine species and individual variation for two species (e.g. Baker 1994; Jurisevic and Sanderson 1994; Crouch 2001). Several species have no geographical variation. No significant temporal variation has previously been described for any Australian honeyeater species, although Baker *et al*. (2001, 2006) found minor changes in the repertoire of the Singing Honeyeater *Meliphaga virescens* over a seven-year period.

In this study I have used Catchpole and Slater's (1995) definitions of song, call, repertoire, phrase, syllable and element. A repertoire is the entire vocal output from a bird including songs and calls. A song is a long, complex vocalisation made up of a series of phrases, given by males to proclaim territory or for mate attraction. A song phrase is a short sequence of syllables that occur together in a particular pattern separated from the next phrase by a pause. A call is shorter and simpler than a song and may be given by both sexes. A syllable is a short unit of sound, and an element (or note) is an individual unit represented by a single trace on a sonogram.

Regent Honeyeater songs are given by males, often with elaborate head bobbing movements and incorporating bill snapping (Higgins *et al*. 2001). A number of authors (summarised in Veerman (1991) and Higgins *et al.* (2001)) have described the song with often conflicting accounts, which may reflect geographical and temporal variation which this study shows can be significant over many years. In general, the songs are relatively soft, intricate and melodious. Regent Honeyeaters are more vocal in the non-breeding season (e.g. Ley and Williams 1994).

Female Regent Honeyeaters are duller in plumage than males and have a smaller bare facial patch, which enables voice comparisons to be made between the sexes. Deren (1999) and Lay (2002) studied the vocalisations of captive Regent Honeyeaters at Taronga Zoo in Sydney, New South Wales. They noted that bill snaps were incorporated into songs or preceded them, and were given only by males. This indicates that song recordings of wild birds that include bill snapping are probably from males.

Calls given by both sexes include a repeated bell-like or mewing 'ping-ping-ping' or 'chink-chink-chink' which may serve as a greeting call, an excitement call, or an alarm call, and can be given simultaneously by a group of birds. (e.g. Ley 1990; Bounds *et al.* 1996; Pizzey 1997; Higgins *et al.* 2001).

Mimicry by Regent Honeyeaters, especially of Red and Little Wattlebirds (*Anthochaera carunculata* and *A. chrysoptera* respectively) has been outlined by Veerman (1992, 1994) and Ley and Williams (1998) and others, but occurs infrequently. Mimicry is rare in Australian honeyeaters, and has been reported in only half a dozen species (Higgins *et al.* 2001).

Juvenile begging calls have been described in Veerman (1991) and elsewhere and may be similar to those of juvenile Red Wattlebirds. E. Collins (pers. comm.) suggests that the young quickly learn to give adult-type vocalisations.

Playback of song and mewing calls recorded in 1995 at Capertee Valley elicited more response from Regent Honeyeaters in Capertee Valley in 1996, than from Regent Honeyeaters near Armidale the same year (Geering 1998), indicating that the birds were more sensitive to calls of their direct neighbours, than to calls of birds 300 kilometres distant. The 1995 taped song phrases did not attract birds in 2008 at Capertee Valley, however birds were attracted by the mewing calls (D. Geering, T. Mason, pers. comm.).

No predawn vocalisations have been reported for the Regent Honeyeater, and Oliver (1998) noted that from May to October 1994 at the Warrumbungles and Howes Valley in New South Wales, Regent Honeyeaters were 10–15 minutes later in becoming active and vocalising, than were most other bird species.

Movements and management

Regent Honeyeaters can live for more than 10 years (banding data, D. Geering, pers. comm.) and they feed mainly on nectar and insects in box-ironbark woodlands (Higgins *et al.* 2001). They are thought to be nomadic and small flocks follow the flowering patterns of their favoured eucalypt species but it is unclear if these movements also involve regular seasonal migration (Higgins *et al.* 2001). Nesting birds often return year after year to the same location (Ley *et al.* 1996; Geering and French 1998). Recoveries and resightings of banded birds show occasional long-distance movements of up to 534 kilometres between Chiltern, Capertee Valley, near Armidale and near Warwick (Fig. 1), (Geering 2003a and b; Mason 2008; banding data, D. Geering, pers. comm.). With only a limited number of resightings of banded birds, it is not known if these long-distance movements are isolated cases or indicate a regular exchange between breeding populations. Regent Honeyeaters travel roughly north-south along the Great Dividing Range, and also have an east-west link with coastal areas possibly in the non-breeding season (banding data, D. Geering, pers. comm.), but generally the extent of these movements is poorly understood.

The National Regent Honeyeater Recovery Team was formed in 1994 after the species was declared nationally endangered. Management policy has been difficult to formulate because it is not clear if Regent Honeyeaters form one single population or if they have diverged into several smaller more isolated groups (Environment and Conservation 2004). One finding that supports the concept of a continuing link between the three main population groups was a nuclear and mitochondrial DNA study done in 1995 that showed no significant differences in the genetic makeup of Regent Honeyeaters from Armidale, Capertee Valley, Canberra and Chiltern (Christidis and Norman 1997). An alternative way of investigating possible species divergence is to look for geographical variation in vocalisations from different locations.

Captive breeding program

To boost the dwindling numbers of Regent Honeyeaters (there are an estimated 500–1500 birds left in the wild) a captive breeding program was begun in 1995, with 10 nestlings taken from the wild in New South Wales and Victoria, and reared successfully at Taronga Zoo in Sydney to produce young of their own. Seven Australian zoos are now linked to this project and as at April 2008 there were 73 captive-bred birds. In May 2008, 27 captive-bred birds aged 1–7 years were released back into the wild at Chiltern to mingle with six wild birds (Ingwersen 2008). Twenty-three of the captives had been reared at Taronga; the other four were raised in other zoos but were housed with Taronga birds for one month prior to release (Shedden 2008). Nine first-year captive-bred birds had previously been released in Capertee Valley in 2000 and of those four were known to have died soon after release.

Regent Honeyeaters that have been raised in captivity have vocalisations unlike their wild counterparts, and may incorporate some of the sounds they hear from their exotic zoo neighbours (M. Shiels, pers. comm.; D. Geering, pers. comm.; Deren 1999; Lay 2002; Cherry and Kelly 2008). Taped songs or calls of wild Regent Honeyeaters have not been used to 'teach' the captive birds (M. Shiels, pers. comm.). In 1997 three first-year Regent Honeyeaters were captured in Capertee Valley and added to the Taronga Zoo population to broaden the genetic base (D. Geering pers. comm.), but it is not known to what extent their wild vocalisations persisted in the captive population. Lay (2002) found similarities in some of the harmonically-rich mewing sounds produced by both wild and captive birds, but compared only those sounds that were similar and not those that were dissimilar. Vocalisations of captive-bred Regent Honeyeaters are described in Results.

METHODS

Song recordings

Regent Honeyeaters were recorded over several days in July 2008 by Howard Plowright and Ed McNabb at Chiltern and Bendigo in Victoria using Sound Devices 702 and Fostex FR-2 LE recorders, Sennheiser ME64 microphones and Bushvoice parabolas. These recordings included vocalisations from both wild and newly-released captive-bred birds. Recordings of wild birds were made by me at Capertee Valley over a number of days in July, August and September 2008, and at Torryburn near Armidale over two days in November 2008 using a Sound Devices 702 recorder and an Olympus LS-10 recorder and Sennheiser ME67 gun microphone. A search was made world-wide of public and private archives for earlier sound recordings of Regent Honeyeaters, resulting in recordings from 1977–2004 being contributed by Bill Flentje, Fred van Gessel, Stuart Fairbairn, Daniela Lay, Graham Chapman, Damon Oliver, Roger Handy, Andrew Skeoch, Beth Williams, David Stewart, Judy Wiles and John Courtney, using a variety of recording set-ups. A total of 19.61 hours of recordings and 3125 song phrases have been analysed for this study (see Table 1).

Analyses of sounds

The available material was analysed using BIAS Peak LE 5.2 audio editing software on an Apple iMac OSX computer, and noise reduction software was used where necessary.

TABLE 1

Details of recordings used in this study. For Chiltern, w = wild and r = released.
Total number of phrases from wild birds analyzed = 3125, from 19.61 hours of recording.

Location	Date	Recordist	Length of recording (minutes)	No. of birds present	Sound quality	Total song phrases analyzed	Song phrase types
near Glen Innes NSW	Sept. 1977	John Courtney	15.1	2	good	78	4
Widden Valley NSW	Apr. 1981	Fred van Gessel	1.1		fair	32	5
Wollembi NSW	Sept. 1983	Fred van Gessel	1.2		fair	20	3
Bendigo Vic	May 1985	Bill Flentje	24	1-3	fair	17	4
Widden Valley NSW	Oct. 1986	Fred van Gessel	1.2		good	21	4
Canberra ACT	Oct. 1987	Graham Chapman	3.5		good	20	3
near Armidale NSW	Jul. 1991	Beth Williams	29	8+	poor	-	
Howes Valley NSW	May 1994	D.Oliver/R.Handy	9	152	fair	11	5
Warrumbungles NSW	June 1994	Damon Oliver	90	40-50	poor	28	5
Chiltern Vic	Apr. 1985	Andrew Skeoch	3	2-3	good	31	5
Capertee Valley NSW	Oct. 1995	Fred van Gessel	2		good	33	5
Vincentia NSW	Apr. 1997	Graham Chapman	6		good	62	3
Capertee Valley NSW	Mar. 1997	Stuart Fairbairn	11	8+	good	68	5
Capertee Valley NSW	Jun. 1997	Vicki Powys	93	50	good	344	5
Taronga Zoo, Sydney NSW	Apr-Aug. 2002	Daniela Lay	7.8	10	fair	-	
near Armidale NSW	Aug. 2004	Judy Wiles	3.5	3+	fair	17	4
Capertee Valley NSW	Sept. 2004	Vicki Powys	2	4-5	fair	16	3
Capertee Valley NSW	July-Sept. 2008	Vicki Powys	420	50	good	1748	6
Chiltern Vic	Jul. 2008	Ed McNabb	40	2-10	good	59w : 72r	2 w
Chiltern Vic	Jul. 2008	Howard Plowright	13	2-10	good	24w : 112r	2 w
Bendigo Vic	Jul. 2008	Howard Plowright	4	2	good	45	3
Taronga Zoo, Sydney NSW	Sept. 2008	Stuart Fairbairn	7	2	good	48	1
near Armidale NSW	Nov. 2008	Vicki Powys	378	10-12	fair/good	451	6

Broadly similar song phrases were aurally collated as Peak files for each location and date, then representative sonograms were printed and sorted into matching groups for further visual analysis. Original sound files were also scanned using Raven Lite 1.0 sound analysis software (Cornell Lab of Ornithology 2003–2006) for combined aural and visual analysis. Elements and syllables were analysed by hand drawing them onto tracing paper, and laying those over existing sonograms for a visual assessment. Some song phrases were also printed onto tracing paper for direct comparisons. Final sonograms were prepared using 1.6 second Peak sound clips and Raven Lite 1.0 with settings of high contrast, variable brightness, and sharpness at 602. (Sonograms can be read like a musical score from left to right; the vertical axis shows frequency (pitch) and the horizontal axis shows time elapsed. Beak snaps are shown by vertical lines.) Raven png files were annotated using Adobe Photoshop Elements 4.0. Figure 1 shows recording and breeding sites. Many of the available recordings were less than perfect and showed reverberation, poor definition and overlapping calls, so an automated computer analysis of song phrases was not attempted.

In order to establish what length of recording might be necessary to determine the song repertoire from any one location, I compared the repertoire of solo singers with the repertoire from many birds, from good quality recordings made by me in Capertee Valley in 1997 and 2008. On both occasions sustained calling from randomly selected birds within a population of up to 50 birds had been sampled. A combined visual and aural assessment was made where 245 song phrases were printed as sonograms (some on tracing paper) and overlaid to compare them, followed up by an aural assessment of a further 5.3 hours of recordings to see if any new phrases were heard (see Table 2).

RESULTS

Repertoire

At Capertee Valley in 1997 and 2008 where long song sequences were studied, there was a high degree of matching of song phrases both within the repertoire from one bird, and between the repertoires from many birds, for any one year (see Fig. 2 and Table 2). Incorporated beak snaps, syllables and spacing between syllables were always closely matched except where a phrase had been abbreviated. At all locations where samples of continuous singing were available, the main repertoire became apparent in 1–2 minutes because song phrases were constantly alternating. In 1997 the full repertoire of five song phrases showed up in sustained singing from one bird that had been recorded at random, in less than a minute. In 2008 where six different song phrases occurred, four of those occurred in greater than 97 per cent of the phrases analysed, and those four phrases showed up in the song repertoire of one bird in less than two minutes.

Elements

An attempt was made to assess song phrases from all locations/years at the level of elements, and in all a total of 144 different elements was found. The number of elements at any one location/year was 10–30. As an example, I compared the elements between Armidale 2008 (excluding one lone bird that sang Capertee-style phrases), and Capertee Valley 2008. There were 22 elements found in the Armidale song phrases and surprisingly, none of these matched with the 30 elements found in the Capertee song phrases. By comparison, 11 of the 14 elements found at Chiltern, and 14 of 18 elements found at Bendigo in 2008, matched with the 30 Capertee elements. At all locations there was little evidence of re-juggling of old elements to make new song phrases. Generally new phrases had new elements, which suggested that the number of elements for Regent Honeyeater song was potentially unlimited. Almost as much information could be gleaned by a comparison of entire song phrases, as could be found by an analysis of the component parts.

Song phrases

For wild birds, 24 different main song phrases (not including minor variants) were identified from the available recordings over the 31-year period 1977–2008. Eleven of those phrases are illustrated in Figs 2–12. Two to six different phrases occurred at any one location, and where groups of birds had been recorded much localised song sharing was evident, with one exception (Armidale, see below). Song phrases were 0.5–1.5 seconds in length and incorporated a variety of relatively soft melodious notes in a phrase of 3–7 syllables whose fundamental frequency was within the range of 1–3.5 kHz.

Figure 1: *Map showing locations mentioned in this study.*

TABLE 2

Analysis of song repertoire for Capertee Valley in 1997 and 2008. In 1997 there were five stereotyped song phrase types for both solo and group singing. In 2008 there was a different repertoire. Four stereotyped song phrase types were found for solo and group singing and greater than 97% of song phrases from 1507 samples were of those four types.

Date	Solo or group	Track length (minutes)	No. of song phrases	Song phrase types	Analysis method
12 June 1997	solo	1:26	14	5	visual + aural
10 June 1997	group	8:48	68	5	visual + aural
10-12 June 1997	combined	82:45 (35 tracks)	262	5	visual + aural
3 July 2008	solo	1:25	15	4	visual + aural
22 July 2008	solo	1:48	26	3	visual + aural
3 July 2008	group	7:31	140	4	visual + aural
2-3, and 22 July 2008	combined	240	1507	6	80 mins visual + aural; 160 mins aural

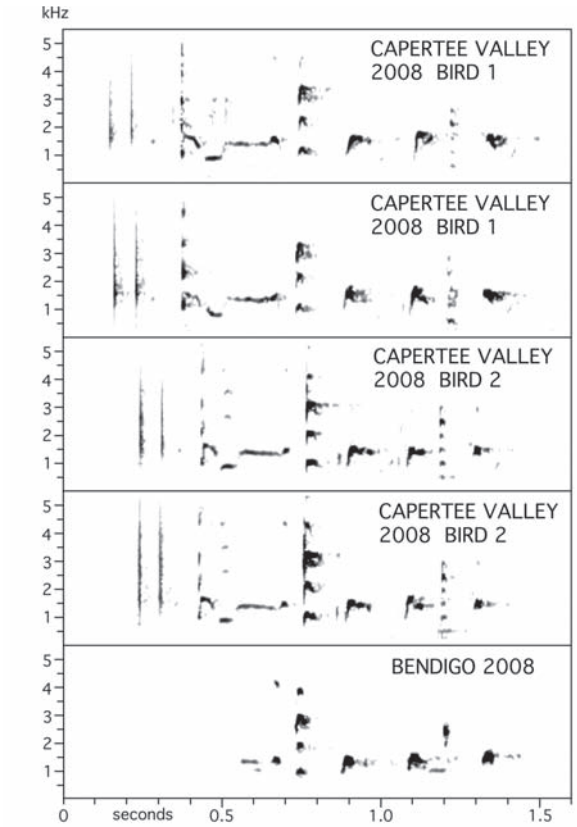


Figure 2. *Shows close matching of song phrase (type K) both within and between repertoires from two different birds at Capertee Valley in 2008, compared with a matching example from Bendigo in 2008. Capertee bird 2 has slightly shorter gaps between syllables compared with bird 1, while the Bendigo bird has not included the initial beak snaps and first syllable.*

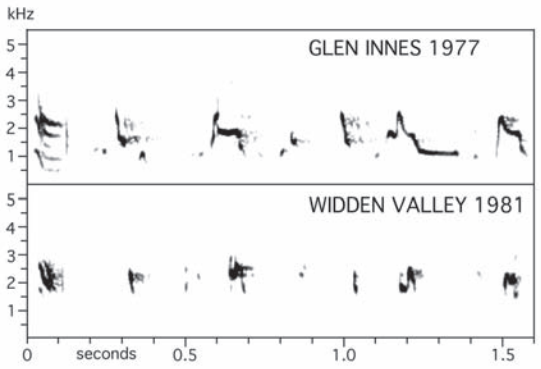


Figure 3. *Song phrase (type A) shared by these locations 1977–1981. Note that the Widden Valley recording had been heavily filtered below 1.5 kHz, which removed the lower frequencies of this phrase.*

Geographical and temporal variation in song phrases were found across the range of the Regent Honeyeater, 1977–2008. Each suite of 2–6 song phrases persisted at any one location for up to six years, although chronological gaps in the available recordings make the upper limit of this time span difficult to estimate. The extent to which a suite of song phrases was shared between different locations was also difficult to gauge because often only short sound samples were available, or samples did not include sustained singing and which may not have included the full repertoire. Assuming that nomadic Regent Honeyeaters learn their songs then carry song phrases from one location to another, geographical movements were then tracked through a study of those songs. The degree to which song phrases were similar or different at widely separated locations may indicate how much time had elapsed since contact occurred between those locations.

The earliest recording available was from 1977 near Glen Innes in northern New South Wales. Two song phrases from that location, types A and B, matched with phrases from Widden Valley in 1981 and 1986 (Figs 3 and 4), indicating links between those areas, at least in the 1970s.

During the 1980s over a seven year period, two song phrases, types C and D, (Figs 5 and 6) were found across a wide geographical area, from Bendigo in western Victoria to Wollombi in the Hunter Valley of New South Wales, again indicating widespread links between those areas.

In the 1990s, five phrases were shared between Howes Valley (1994), Warrumbungles (1994) and Capertee Valley (1995-97) including song phrase types E, F and G (Figs 7, 8 and 9). Type G also occurred at Chiltern in 1995.

Vocalisations recorded at Chiltern and Capertee Valley in July 2008 showed strong similarities in song phrase type H (Fig. 10), suggesting a continuing link between these two population groups. One bird at Armidale in 2008 was also giving this particular phrase (Fig. 10), while all the other Armidale birds sang a different suite of four song phrases (two are shown in Figs 11–12). This suggests that at least one bird had travelled, perhaps recently, from Capertee or Chiltern to Armidale. Four song phrases from Armidale in 2004 and 2008 had remained stable over at least five years and generally were not similar to Capertee or Chiltern, which suggests that the Armidale population has had only limited contact with the Capertee and Chiltern groups, in recent years. A link between Bendigo and Capertee in 2008 was shown in the shared song phrase Type K (Fig. 2). Phrase type H also occurred at Bendigo in 2008. Phrase types H and K were also evident in a brief recording from Capertee Valley in 2004.

It seems likely that song phrases may change gradually over a period of years. However, the record for Capertee Valley (and linked populations at Howes Valley and Warrumbungles) shows one shared suite of five songs in 1994–97, then a completely different suite of songs in Capertee Valley in 2008 (Figs 7–10). Similarly, Chiltern songs had changed completely between 1995 and 2008. A lack of recordings for the intervening years meant that it could not be determined if the change was sudden or gradual.

A 3-note phrase occurred over a 27-year period from Victoria to central New South Wales but was not recorded in the northern New South Wales locations. It is unclear if this was a call or a song phrase, but has been included as a song phrase for this study. At Chiltern in 2008 it seemed to be used as a contact call, whereas in Capertee Valley in 1997 it was used often within sequences of song. It was only occasionally heard at Capertee Valley in 2008.

Calls

A mewing call common to wild birds at all localities comprised a series of relatively loud, variable mewing, pinging or bell-like sounds that were harmonically rich (Fig. 13). These have been variously described as ‘ping’, ‘ding’, ‘wang’, ‘wah’ or ‘mew’ and were given by usually more than one bird in disputes, in social interactions, and as an alarm call. A 3-year-old captive-bred bird (i.d. number 990025) at Taronga Zoo in Sydney also gave the ‘ping’ call in 2002 (Fig. 13), but may have learned that call from wild stock introduced in 1997.

At Capertee Valley in 2008 ten other short calls were recorded but were heard only infrequently. These ranged from a harsh and relatively loud yap, to a very soft ‘ker-lip’ contact call. Short soft trills (0.2 sec) occurred occasionally and were recorded at four locations 1995-2008. At Chiltern in July 2008 a melodious note repeated about five times was used often as a ‘bonding call’ by wild birds, and was different to the ‘ping’ or mewing call (C. Tzaros pers. comm.).

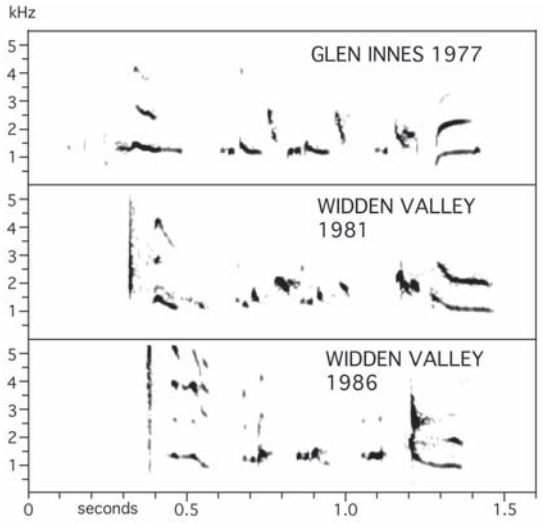


Figure 4. *Song phrase (type B) shared by these locations, with minor variations. The phrase had contracted slightly by 1986.*

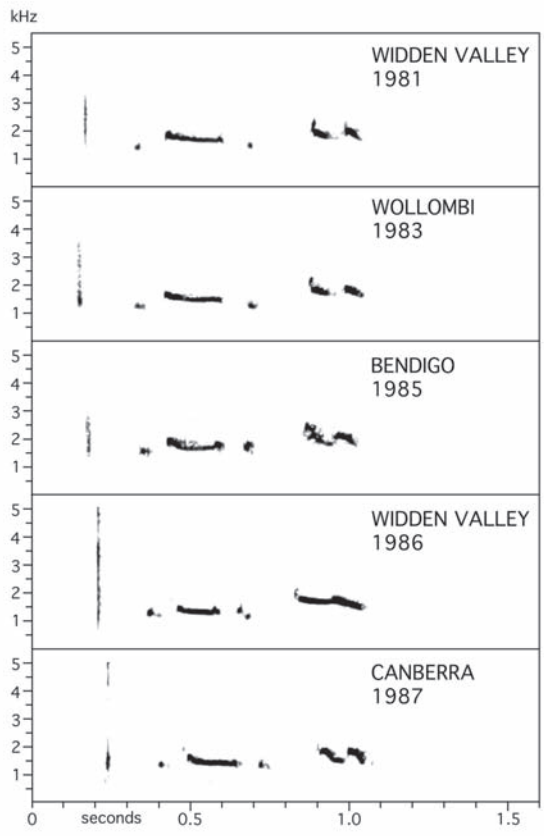


Figure 5. *Song phrase (type C) shared by these locations in the 1980s. This phrase was somewhat similar to the song phrase type G of the 1990s, illustrated in Fig. 9.*

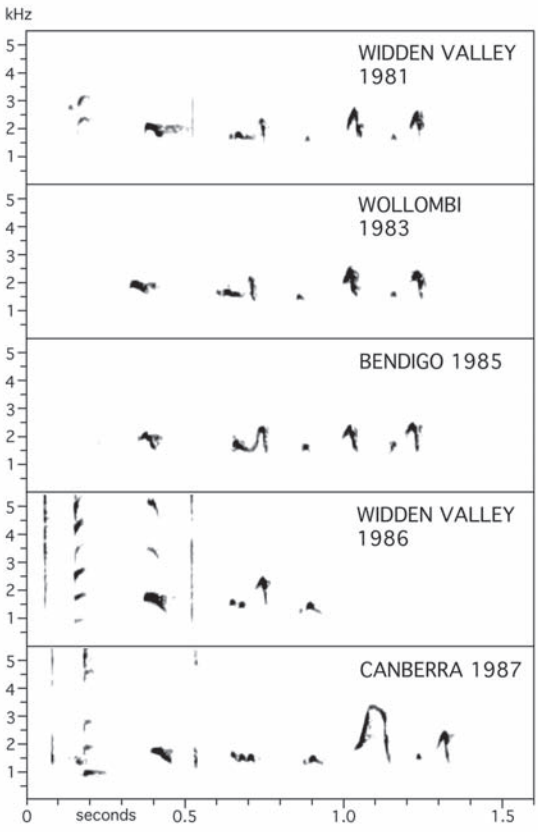


Figure 6. *Song phrase (type D) showing related variations shared by these locations. Widden Valley 1986 shows an abbreviated version of the phrase, while Canberra 1987 shows an emphatic note at 1.1 seconds.*

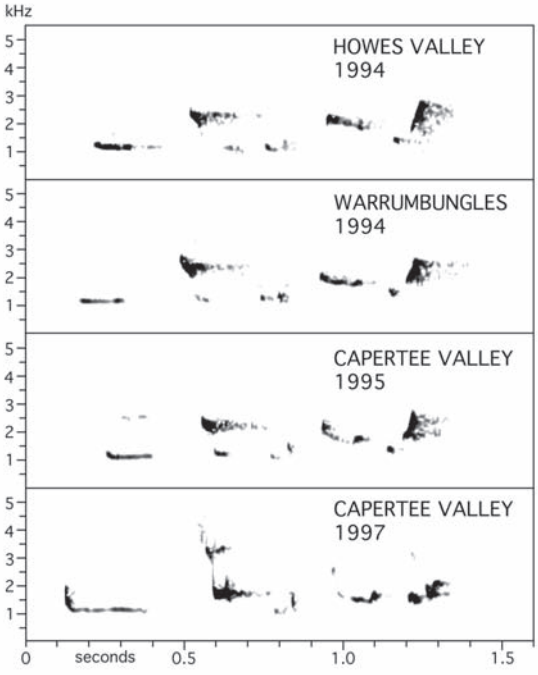


Figure 7. *Song phrase (type E) was shared by these locations 1994–97. Capertee 1997 sample was recorded close to the bird and gives better resolution than the other three samples.*

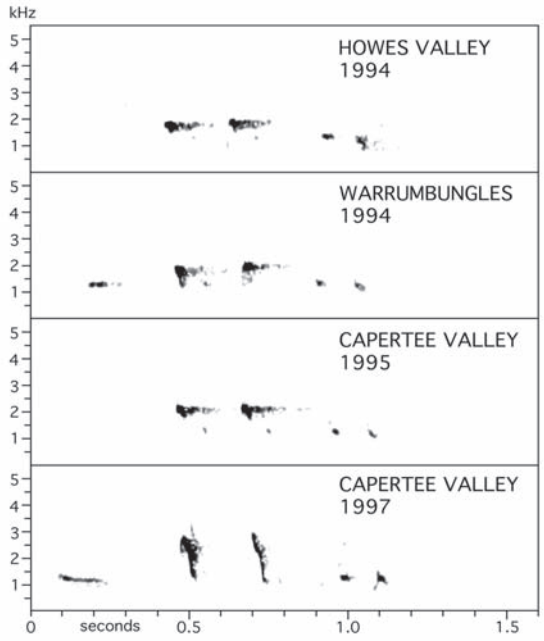


Figure 8. *Song phrase (type F) was shared by these locations 1994–97. Capertee 1997 sample was recorded close to the bird and gives better resolution and more frequency response than the other three samples.*

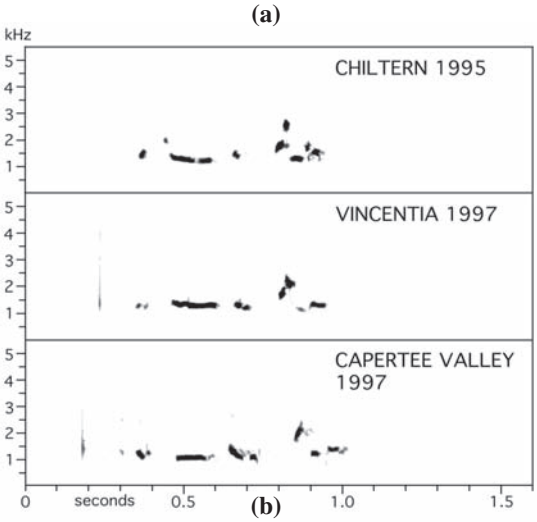


Figure 9 (a) and (b). *Song phrase (type G) was shared by these locations 1994–97.*

Mimicry

Mimicry was recorded twice at Capertee Valley in 2008. One bird mimicked a Red Wattlebird while giving soft song. Another bird which mimicked a Spiny-cheeked Honeyeater *Acanthagenys rufogularis* had been colour-banded six years previously in Warwick where it may have learned the calls (D. Geering and T. Mason, pers. comm.). From the available tapes, mimicry of Red and Little Wattlebirds occurred at Vincentia in 1997, and probably at Chiltern in 2008. Observers at Chiltern reported extensive mimicry of a Little Wattlebird in 1999.

Captive-bred birds

Field workers at Chiltern in 2008 dubbed the aberrant calls and songs of the newly-released captive bred birds as 'Sydney slang'; the vocalisations of the captive-bred were generally harsh and bore no resemblance to the calls and songs of wild Regent Honeyeaters (E. Collins, pers. comm.).

Recordings from Chiltern in July 2008 verified those observations (Fig. 14). Some phrases may have been based on mimicry of other captive zoo birds. One phrase sounded like a Cockatiel *Nymphicus hollandicus* and was given by many of the captive-bred birds. Another phrase sounded like a Bush Stone-curlew *Burhinus grallarius* and was given initially by only one of the captive-bred birds, a four-year-old known as Orange/Mauve. After several weeks two other released birds (first-year males Mauve/Red and Blue/Red) also began to give the curlew call (S. Kelly, pers. comm.). Variants of the mewing call were heard from all captive-bred birds. Beak snaps were given often.

By August 2008 two different newly-released birds at Chiltern (first-year males White/Red and Black/Red) had taken up one of the wild bird calls, the 3-note phrase (S. Kelly, pers. comm.; Cherry and Kelly 2008). A male bird at Taronga Zoo (September 2008) gave a harsh phrase that was different to the Chiltern-released birds, and that phrase was repeated over and over and included beak snaps and an occasional mewing call (Fig. 14).

DISCUSSION

Song learning

Song learning in passerines is complex and the degree to which song is innate or learned varies between species (Catchpole and Slater 1995). Some species learn their songs as juveniles and young adults, while others, especially those where the song repertoire changes over time, also learn songs later in life. Social interaction may also play a role in song learning. Thorpe (1958) and Nottebohm (1968) found that Chaffinches *Fringilla coelebs* reared in isolation gave songs similar to but simpler than those of wild birds, but were able to refine their songs if exposed as juveniles to taped calls of their species. Adult Chaffinches were unable to learn new songs. Juvenile Zebra Finches *Taeniopygia guttata* did not learn from taped calls, but relied on social interaction as part of the song learning process (Eales 1989). Wild adult Village Indigobirds *Vidua chalybeata* that moved to a new area adopted the repertoire of that area and, unlike chaffinches, were able to learn new songs well into adulthood (Payne 1985).

Superb and Albert Lyrebirds (*Menura novaehollandiae* and *M. alberti* respectively) in any one location retain their territorial song for at least 7-20 years (Powys 1995; Robinson and Curtis 1996; Curtis 2005, Powys unpublished data), while Pied Butcherbirds

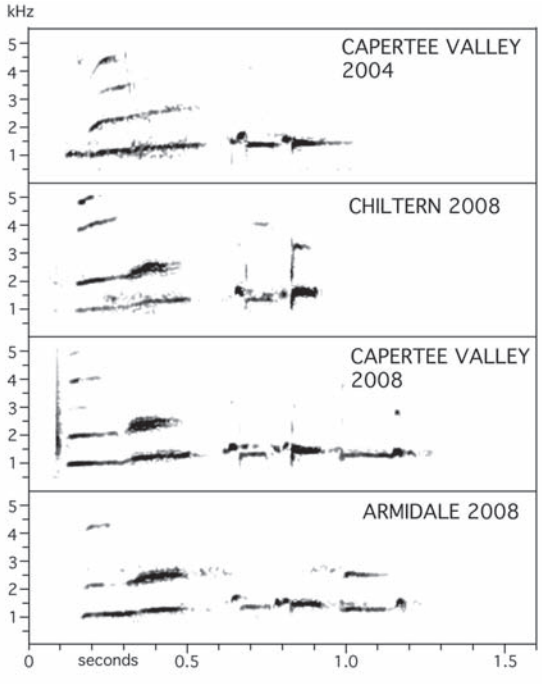


Figure 10. *Song phrase (type H) was shared by these locations 2004–08. Note that only one bird at Armidale sang this particular phrase. An additional syllable was often added at the end of the Capertee and Armidale phrases in 2008.*

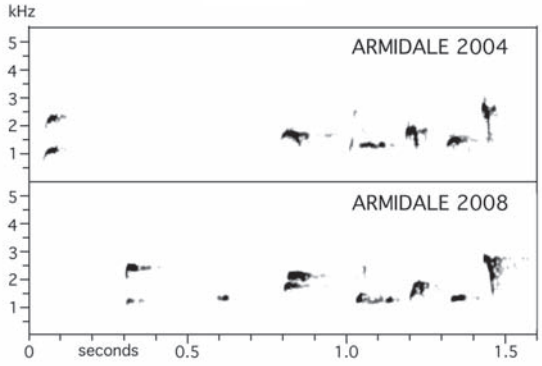


Figure 11. *Song phrase (type I) at Armidale in 2004 and 2008.*

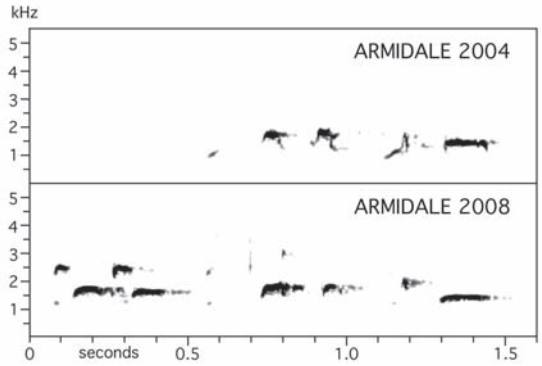
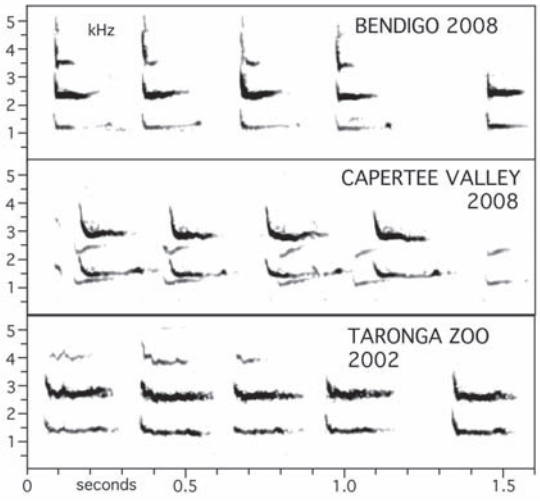
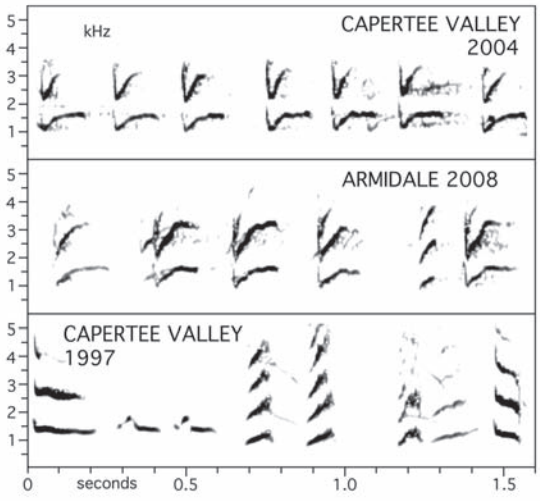


Figure 12. *Song phrase (type J) at Armidale in 2004 and 2008, with additional notes in 2008.*



(a)



(b)

Figure 13 (a) and (b). *'Mewing' calls were common to all locations in this study and were variable at any one location. The Taronga Zoo 2002 call was from a 3-year old male identified as 990025.*

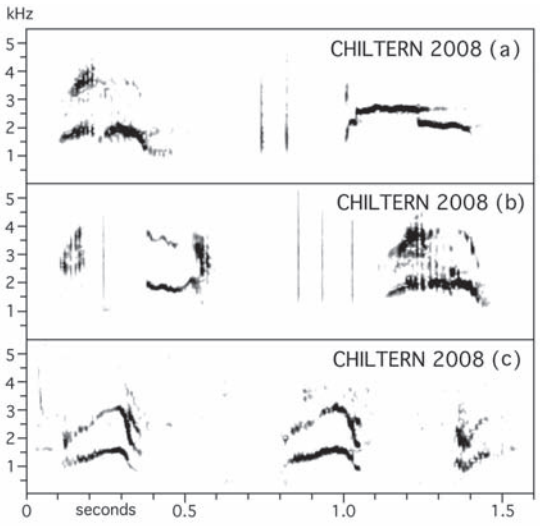
Cracticus nigrogularis change their song repertoire either completely or partially, every year (G. P. Johnson in Higgins *et al*. 2006; Powys 2007; Taylor 2008). The Noisy Scrub-bird *Atrichornis clamosus* of Western Australia may change its song repertoire every few weeks, probably led by one dominant male in a group of up to 10 males (Berryman 2007).

This study shows that groups of Regent Honeyeaters change their songs over a period of years, which could indicate that they can learn new songs later in life. This may be an advantage for the successful integration of captive-bred Regent Honeyeaters into wild populations. It is not known if captive Regent Honeyeaters would learn songs from tapes, or if social interaction is a necessary part of their song learning. The aberrant and harsh vocalisations of the zoo-bred birds may either indicate juvenile song learning through social interaction with their fellow zoo inmates e.g. Cockatiel and Bush Stone-curlew, or alternatively could be thought of as mimicry. Regent Honeyeaters have no obvious auditory template (as do Chaffinches), because the songs of the zoo-bred Regent Honeyeaters are not in any way similar to the songs of wild birds.

Two first-year birds released at Chiltern in 2008 that picked up the 3-note phrase of wild birds indicated that social interaction may be part of the song learning process. Field workers at Chiltern in 2008 noted that only one captive-bred bird (Orange/Mauve) gave the curlew call prior to its release, but after release two other first-year captive-bred birds began giving this call, again indicating song learning in a social context.

For bird song repertoires with an unlimited number of elements or syllables, song matching was unlikely to occur by chance at differing locations (Catchpole and Slater 1995). This paper shows an extensive repertoire for the Regent Honeyeater with a potentially unlimited number of elements or syllables which confirms their ability to invent and learn new elements, syllables and song phrases.

Veerman (1994) has suggested that mimicry by Regent Honeyeaters was used for deception, enabling isolated birds to blend with feeding flocks of larger and more aggressive honeyeater species. However E. Collins (pers. comm.) described a banded



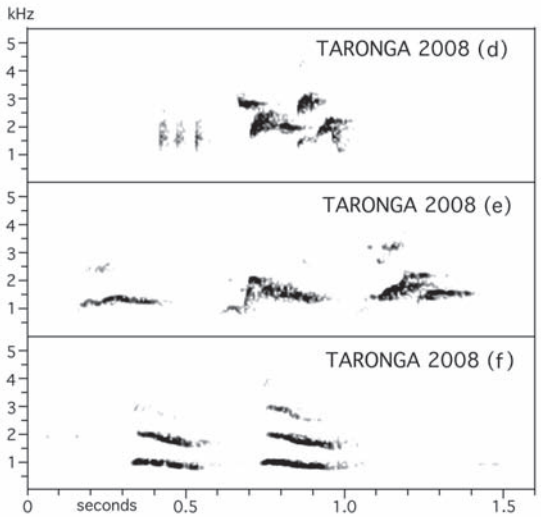


Figure 14. *Vocalisations from released and captive birds: (a) at Chiltern a 'cockatiel' call followed by a 'curlew' call, (b) various calls and 'cockatiel' call, (c) 'mewing' calls. From Taronga Zoo in Sydney: (d) beak snaps and typical call, (e and f) 'mewing' calls.*

bird Yellow/Yellow giving only mimicry of a Little Wattlebird throughout the summer of 1999 at Chiltern, with no Regent Honeyeater calls heard and with no Little Wattlebirds present. At Capertee Valley in 2008 a Regent Honeyeater mimicked a Spiny-cheeked Honeyeater for much of one day, where no Spiny-cheeked Honeyeaters were present and where they seldom occur. These observations suggest that Regent Honeyeaters have the capacity to learn and memorise calls and other sounds for later reuse. Possibly lone birds mimicking other species may have spent some time isolated from their own species. Mimicked species could give further clues as to the movements of Regent Honeyeaters e.g. Little Wattlebirds are often a coastal species.

Ongoing monitoring is needed to determine if released captive-bred Regent Honeyeaters will adopt the wild bird vocalisations, and also to what extent the calls of captive-bred birds might persist in the wild. Conversely it will be interesting to see if wild Regent Honeyeaters adopt any of the captive-bred calls. For wild birds it is not known how long it might take for a long-distance traveller to fully adopt the repertoire of a new location.

Recording of wild Regent Honeyeater songs on a regular basis in the future will also help in understanding nomadic or migratory movements and could be a useful adjunct to banding. More field workers need to learn to use non-invasive tools such as sound recording for ongoing documentation of this endangered species. Further studies are also needed to elucidate the mechanism of the changes in repertoire of the Regent Honeyeater over time.

If taped calls of wild birds were to be used at zoos to try and teach captive Regent Honeyeaters, care would be needed to choose current dialects from the proposed area of release. Taped calls used as an aid for mist-netting of wild Regent Honeyeaters for banding purposes should likewise be of a current and local dialect. Regent Honeyeaters are no longer responding to playback of songs recorded in 1995 (D. Geering, pers. comm.).

Nomadic or migratory?

Nomadic birds by definition wander according to available food resources, while migratory birds undertake predictable annual seasonal movements between a breeding ground and a wintering ground. In species where some individuals migrate while others remain in one locality throughout the year, this is known as partial migration (Berthold 2001; Chan 2001). Regent Honeyeaters are nomadic but it is not known if they are also migratory. Keast (1968) considered Regent Honeyeaters to be only nomadic, but Franklin *et al.* (1989) studied available historical data and have suggested that Regent Honeyeater movements may have two distinct elements: semi-migratory longer-distance movements and local nomadic wandering in search of accessible nectar. This conclusion seems plausible in the light of more recent findings and banding data.

In a study of the possible genetic migratory orientation of Regent Honeyeaters, Cooke and Munro (2000) found a north-east orientation in six captive-born juveniles (first generation Capertee Valley stock) for April–May (autumn), and no specific orientation for June–July (winter). Spring and summer orientation were not tested, and a genetically controlled north-east migratory link between Capertee Valley and coastal areas was proposed. Chiltern to the south-west was not mentioned. Capertee Valley does have sudden influxes of Regent Honeyeaters in June–July with no clear understanding of where the birds have come from. Given that Regent Honeyeaters may have a north-east orientation for the autumn months it follows that they may have come from the direction of Chiltern. A link with Chiltern has been proven in this present study.

It would be interesting to know if Regent Honeyeaters have a reverse south-west orientation during the summer months after breeding, and if birds from Capertee Valley then fly towards Chiltern. Some birds over-winter at Chiltern, as did a small group in 2008. Perhaps migratory instincts are switched on or off according to the availability of food resources. There is a need to monitor the Chiltern-Capertee route more intensively during the autumn months, and where possible to make sound recordings of the travelling birds, which may help to indicate the origin of those birds.

CONCLUSION

This paper has presented evidence of vocal learning in Regent Honeyeaters by demonstrating geographical and temporal variation in wild birds, their ability to mimic, a profoundly different repertoire for captive-bred birds, and the ability of two newly-released captive-bred birds to pick up a song phrase from wild birds. Further study is needed to determine to what extent the mewing-type calls may be innate or learned. This paper also shows that Regent Honeyeaters can be tracked through a study of their songs. There are still close links between the Bendigo/Chiltern and Capertee populations, which had similar 2008 songs, however there may now be less contact with the Armidale group than in 1977–81 because Armidale songs of 2004–08 (apart from one lone bird) were dissimilar to the southern locations. Given that song phrase types only endure for 5–10 years, if discrete populations begin to form at the three core breeding sites this is likely to become evident within that time and would be shown in the increasingly different songs of those populations.

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