

Variation in songs of the White-eared Honeyeater, *Nesoptilotis leucotis* among its four mainland subspecies

ANDREW BLACK AND DAVID STEWART

Abstract

We find differences among the songs of four mainland subspecies of White-eared Honeyeater. Divergence is particularly pronounced across the Eyrean Barrier, i.e. between phylogroups distributed on either side of Spencer Gulf. Such divergence in song provides a potential mechanism for reproductive isolation and the early stages of speciation.

INTRODUCTION

Until recently, three subspecies of White-eared Honeyeater, *Nesoptilotis leucotis* were recognised: the nominate, forest-occupying *N. l. leucotis* east of the Great Divide and extending through southern Victoria into the south east of South Australia, *N. l. novaenorcaiae* in southern Western Australia, Eyre Peninsula and the eastern mallee, inland of the Great Divide, and *N. l. thomasi* on Kangaroo Island (Schodde and Mason 1999).

Taxonomic revision has been obliged by the phylogeographic study of Dolman and Joseph (2015), who found a deep divergence within the species at the Eyrean Barrier (present day Lake Torrens-Spencer Gulf), i.e. dividing the range of what was then regarded as the subspecies *N. l. novaenorcaiae*. Their findings suggested the possible development of cryptic speciation at the Eyrean Barrier but could not exclude significant gene flow between the two phylogroups. Yet they argued that at least subspecific division was warranted there and accordingly asserted that *N. l. novaenorcaiae* can only include populations to the west of Spencer Gulf.

Prompted by that finding, Black (2018) showed that Eyre Peninsula and eastern mallee populations, the latter including those of the Flinders Ranges, are phenotypically distinct from one another and are allopatric, separated across Lake Torrens and Spencer Gulf.

Black (2018) acknowledged the consistently asserted distinction between the eastern mallee and forest phenotypes from still further east in south-eastern Australia and recognised the former as *N. l. depauperata*, following Mathews (1912).

Within the western phylogroup, Western Australian and Eyre Peninsula populations are also allopatric, separated by the Great Victoria Desert and across the Nullarbor Plain. The Eyre Peninsula population is now recognised as *N. l. schoddei* (Black 2019, Gill and Donsker 2019).

The known distribution of the White-eared Honeyeater is shown in Figure 1.

We here address one factor pertinent to the question of potential gene flow between the two phylogroups by asking whether song divergence has occurred. Divergence in song may contribute towards reproductive isolation and the early stages of speciation (Price 2008, Kleindorfer *et al.* 2013) and can parallel and even drive genetic divergence (Päckert 2018).

The White-eared Honeyeater has a rich repertoire of song that is considered loud, ringing, far

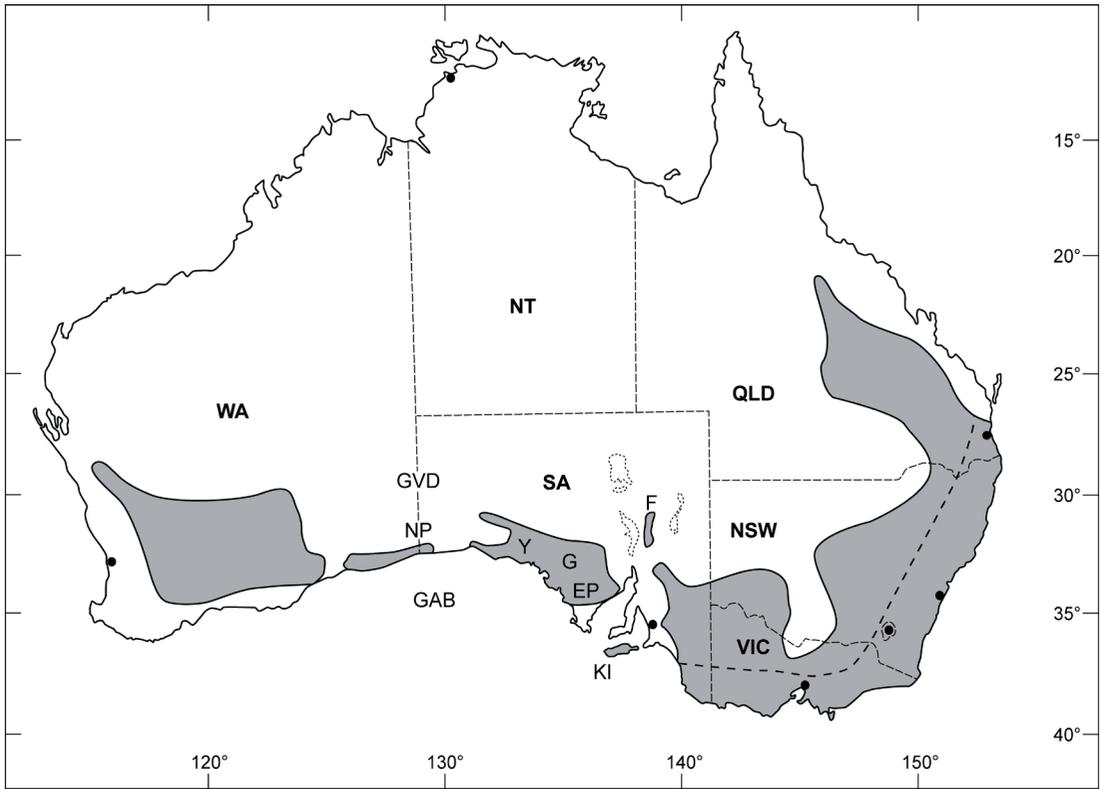


Figure 1. Map showing the known distribution of White-eared Honeyeater. From left to right: WA *N. l. novaenorciae*, showing a small discontinuity northeast of Israelite Bay between Balladonia and Caiguna and its extension south of the Nullarbor Plain (NP) into far west SA; separated by much of the Great Victoria Desert (GVD) from *N. l. schoddei* of the Yellabinna (Y), Gawler Ranges (G) and Eyre Peninsula (EP); *N. l. depauperata*, including the small Flinders Ranges (F) outlier; and *N. l. leucotis* with the putative zone of interaction between *N. l. depauperata* and *N. l. leucotis* indicated by a dotted line. Also shown is the Kangaroo Island (KI) population *N. l. thomasi*.

carrying and distinctive (Officer 1964, Simpson and Day 2004, Slater 2009, Menkhorst *et al.* 2017).

Higgins (1992) (cited in Higgins, Peter and Steele 2001, pp 788-9) reported his analysis of the honeyeater's voice in a detailed study in Brisbane Water National Park north of Sydney. He described and named eight "calls", given in varying frequency throughout the year. He did not analyse the function of individual calls or define the contribution of any to the honeyeater's song. The calls he recognised were: 'chew' and 'two-note' ("tch-tchew"), the most frequent; 'clock', 'one-note' and 'scolding' less frequent; and 'rapid clock', 'trill' and 'chip' infrequent. Those calls may be recognised as consisting of repeated elements of one or two syllables.

Other descriptions of the honeyeater's voice vary, although many acknowledge the 'chew' (transcribed as 'tew', 'choor', 'chung', 'chiong' etc.) and the 'clock' ('chwok', 'chock', 'churruk').

As among songbirds generally, this species of honeyeater's song is made up of a sequence of phrases consisting of separate elements, each of which may be repeated. It has thus given rise to further interpretations, such as: 'chock-u-whit', 'kwitchu', 'chock-up', 'cheery bob', 'come-up', 'do-it-well' (North 1906, Officer 1964, Morcombe 2003, Simpson and Day 2004, Slater 2009, Pizzey, Knight and Pizzey 2012, Menkhorst *et al.* 2017).

The majority of descriptions given above are of the voice of the eastern, forest-dependent White-eared Honeyeater, the nominate subspecies *N.*

l. leucotis, although Pizzey, Knight and Pizzey (2012) found that “inland populations” had “lighter calls of more syllables”, including mellow ‘cherrywheet’ and quick ‘chittagong’. Slater (2009) described a five-noted chime in inland Queensland and a call “in west” [= Western Australia perhaps] as ‘tew-wh-wh’.

This study employs the descriptive terms of Higgins (1992) in reviewing samples of the voice of the four mainland subspecies, which henceforth we indicate by their subspecific epithets, namely: in the eastern phylogroup, *leucotis* of eastern forests and *depauperata* of the eastern mallee, and in the western phylogroup, *novaenorciae* of Western Australia and *schoddei* of Eyre Peninsula.

METHODS

We reviewed a selection of recorded voice of White-eared Honeyeaters made by D. S. (Stewart 2018) from the two mainland subspecies within each phylogroup, thus: from *leucotis* (nine localities, total recording duration 556 seconds); *depauperata* (five localities, duration 383 seconds); *schoddei* (three localities, duration 706 seconds); and *novaenorciae* (seven localities, duration 968 seconds). Additional recordings were reviewed from four eastern localities within the putative zone of interaction between forest and mallee populations; Kroombit Tops in Queensland, Coonabarabran in New South Wales, and Bendigo and Dergholm in Victoria.

All recordings were edited to comprise only what we regarded as song, thus eliminating simple contact and similar calls. As a result, the scolding or chip vocalisations of Higgins (2001), while regularly represented, are not considered in the analysis.

The authors have identified each reviewed sound file individually. All will be archived in the Australian National Wildlife Collection. Each author made an independent assessment of song recordings and assigned individual

phrases in each recording to one of Higgins’s (1992) identified call-types, where possible, but if they could not be so assigned they were referred to a separate category. We did not consistently distinguish calls of ‘one note’ and therefore limited our categories to six: ‘chew’, ‘two note’, ‘clock’, ‘rapid clock’, ‘trill’ and ‘other’.

RESULTS

Our findings are summarised in Table 1. Notes provide examples of our transcriptions of the calls, indicating the variety of ways that they can be interpreted by different listeners, including those cited above, or even by the same listener under differing circumstances.

Voice of *N. leucotis leucotis*

Our review of calls of the eastern forest population allowed us to reconcile them generally with the call-types of Higgins (2001). The ‘chew’ call was well represented and was transcribed in a variety of ways, tsiew, chiew, djieeu. Examples of ‘two note’ we heard as djii dong, djii djong, gee-bob, also djuii, wudda weed, wheera whi, djoh-djoh, djaan-widdu, chiddu-whee. ‘Clock’ and ‘rapid clock’ we heard mostly as ock.

Voice of *N. l. depauperata*

We found songs and their components in the eastern mallee population to resemble those of the nominate subspecies closely but found distinction indicative of separate dialects. The ‘chew’ call we transcribed as chiew or chiew. We also recorded calls of djoh. The ‘clock’ sounded more like glog. Calls from what we took to be the intergradient zone were generally closer to those of the nominate subspecies, as was one from the Little Desert, perhaps within that incompletely identified zone (Schodde and Mason 1999). One recording of calls from Dergholm, near Casterton in southwest Victoria, initially considered an intergradient locality, was so like that of the nominate subspecies that we inferred that it probably lay within the latter’s distribution.

Table 1. Summary of the calls from all localities among four mainland subspecies of White-eared Honeyeater, showing assignment of individual calls to five of the categories of Higgins (1992), where possible, and variation in notation used to describe the calls.

Locality	chew	2note	clock	rapid	trill	other	notes
<i>N. l. leucotis</i>							
Dergholm NP Vic	x						see text; tsiew, chiew
Angahook NP Vic	x	x	x		x		djeeu, djeeu-chi
Broadford Vic	x	x		x	x		djii dong
Yellingbo Vic		x					dju-iit
Bunyip Vic		x					djii-dong, jiddong, gee bob
Rotamah Island Vic	x	x					djoh djiddih
Nimmitabel NSW		x					gwee-gu, gee bob
Numeralla NSW	x	x					djii dong
Tianjarra Falls NSW		x					widdee, djan-widdu
Intergrade zone							
Kroombit Tops Qld	x	x					djeu djeu, dji-djii-do-dji
Coonabarabran NSW		x					cheery bob
Bendigo Vic	x	x					weearr-wui
<i>N. l. depauperata</i>							
Little Desert Vic	x	x		x			djoh-djoh, djit-djoh, glog-glog-glog--
Comet Bore SA	x		x	x			chiow, jiaow
Pertendi Bore SA	x	x			x		chock up
Hattah Lakes NP Vic		x					cheery bob
Gluepot SA	x	x		x			jee dubud
<i>N. l. schoddei</i>							
Lake Gilles CP 1		x				x	djirri-du, djii du-ip chip, djii-j-uwee
Lake Gilles CP 2	x	x					buzzing chiow, chog-up
Lake Gilles CP 3	x	x		x			whit-oc, oc-oc-oc-oc--, chop-eet, chog-up
<i>N. l. novaenoriae</i>							
Mundrabilla 1	x						buzzing chieew
Mundrabilla 2	x	x				x	Ip-ip-ip-ip--, ip-chiow-chiow
Eyre Bird Observatory	x					x	chiong cheer weer-cho
Great Western Woodlands 1	x	x				x	two varieties of chew, da-dung da-dung, chiong-chiong
Great Western Woodlands 2	x	x	x	x		x	accelerating chog-chog--, chog-up chog-up --, chiow-chiow-chiow--
Norseman	x						low pitched chiow
Dryandra	x	x		x		x	variable repetitive chiow, long complex phrases

Voice of *N. l. schoddei* and *N. l. novaenoriae*

These songs differed substantially and, while most calls of *N. l. schoddei* could be assigned to one of the categories of Higgins (2001), some could not. The differences were even more pronounced in the case of *N. l. novaenoriae*, where almost all calls were at least subjectively different, and many were more complex than any heard among populations of the eastern phylogroup.

DISCUSSION

We have assessed recordings (Stewart 2018) from many localities taken in different seasons and under a variety of conditions; in the absence of a standardised protocol, we make no statistical comparisons.

In considering each population separately, the authors were in close agreement in finding the *leucotis* sample of eastern forests to be compatible with Higgins's study, all recorded calls being recognised as closely related to 'chew', 'two-note' or 'clock'. The second note of two-note calls was of higher pitch in some and lower in others. Either syllable might be slurred. We arrived at similar agreement with the *depauperata* sample from the eastern mallee, where 'rapid clock' (glog) calls were also well represented. Subjectively, calls from the mallee seemed lower pitched and less sharp or harsh than those from the forest population. Our rendition of glog might refer to the frog-like call that White (1913) reported from the mallee and which Higgins (in Higgins, Peter and Steele 2001) found particularly inappropriate for the species. The 'chew' call was again found to vary and was annotated in several ways.

The *schoddei* calls included a further variant of 'chieew' (see below), a two-note form and others difficult to classify, more complex and of three or four syllables. The large sample of *novaenoriae* calls were even more complex and variable so that agreement on their naming was not achieved between the authors. Three variants of the

'chew' call were noted, high pitched 'chieew' and lower 'chew' and 'chiow'. A number of rapidly repeated elements were heard that did not correspond to 'rapid clock'. At least 30% of the recorded voice of *novaenoriae* could not be identified in Higgins's system and most calls were at least subjectively different. A call present in both *novaenoriae* and *schoddei* is a high-pitched 'bzz' within the otherwise designated 'chieew'. The 'bzz' was rare otherwise, although it was recorded at one *depauperata* site.

It is uncertain to what extent some of the differences we have detected might be attributed to local or even individual variation, rather than from distinct regional dialects. It is clear nonetheless that there is much scope for further analysis of the variation in song among White-eared Honeyeaters. Much more extensive sampling is desirable although some trends are clear. We found subjective differences between the voices of *leucotis* and *depauperata* and several recordings from assumed regions of intergradation sounded more like those of the nominate subspecies. There is uncertainty about the zone of interaction between those subspecies (Schodde and Mason 1999) and one sample included among those of *depauperata* from the Little Desert Victoria also sounded close to the call of *leucotis*.

Songs of *novaenoriae* are certainly more complex and variable than eastern examples. They contain syllables that we did not find represented in Higgins's system of calls derived from eastern forest populations or indeed from any other population. The considerable repertoire of *novaenoriae* song contained a number of three and four syllable phrases and many repetitive phrases that seemed unique. The song of *schoddei* also include unclassified calls and both *novaenoriae* and *schoddei* samples include a 'bzz' call that appears to be rare elsewhere.

CONCLUSION

We have detected pronounced differences between songs of eastern and western

phylogroups, the latter being more complex and containing apparently unique elements and sequences. Within the eastern phylogroup, dialectic differences between *leucotis* and *depauperata* calls are in keeping with their phenotypic distinction and taxonomic ranking. The sample of *schoddei* calls has affinity with the more widely sampled but more complex calls of *novaenorciae*, which we find differ considerably from all others. Further research is needed, to test voice distinctiveness of each of the four subspecies.

The substantial divergence between songs of western and eastern phylogroups might well provide a behavioural mechanism that is developing a pre-mating barrier between them (Price 2008). This requires further testing and we recommend firstly the objective sonographic analysis of individual elements and phrases. Long term study will be necessary to record voice among different populations under more standardised conditions and to test the responsiveness of individuals to calls of the same and different populations (Kleindorfer *et al.* 2013).

ACKNOWLEDGEMENTS

We have enjoyed fruitful discussions on this subject with both Leo Joseph and Dick Schodde, the latter suggesting the potential value of undertaking the present study. We are grateful to both for their constructive suggestions for amendment to the submitted draft and to Belinda Cale for preparing the map Figure 1.

REFERENCES

- Black, A. 2018. Notes on the distribution and taxonomy of White-eared Honeyeaters in South Australia. *South Australian Ornithologist* 43: 17-26.
- Black, A. 2019. A new subspecies of White-eared Honeyeater *Nesoptilotis leucotis* (Meliphagidae). *Bulletin of the British Ornithologists' Club* 139: 164-172.
- Dolman, G. and Joseph, L. 2015. Evolutionary history of birds across southern Australia: structure, history and taxonomic implications of mitochondrial DNA diversity in an ecologically diverse suite of species. *Emu* 115: 35-48.
- Gill, F. and Donsker, D. 2019. *IOC World Bird List (v9.2)* doi: 10.14344/IOC.ML.9.2
- Higgins, P. J. 1992. Unpublished MSc thesis, University of Sydney.
- Higgins, P. J., Peter, J. M. and Steele, W. K. (eds) 2001. *Handbook of Australian, New Zealand and Antarctic birds. Volume 5, tyrant-flycatchers to chats*. Oxford University Press, Melbourne.
- Kleindorfer, S., Evans, C., Mihailova, M., Collembelli-Négrel, D., Hoi, H., Griggio, M., Mahr, K. and Robertson, J. 2013. When subspecies matter: resident Superb Fairy-wrens (*Malurus cyaneus*) distinguish the sex and subspecies of intruding birds. *Emu* 113: 259-269.
- Menkhorst, P., Rogers, D., Clarke, R., Davies, J. N., Marsack, P. and Franklin, K. 2017. *The Australian bird guide*. CSIRO Publishing, Clayton South, Victoria.
- Morcombe, M. 2003. *Field Guide to Australian birds*. Revised edition. Steve Parish Publishing Pty Ltd, Archerfield, Queensland.
- North, A. J. 1906. *Nest and eggs of birds found breeding in Australia and Tasmania. Volume II*. F. W. White, Sydney.
- Officer, H. O. 1964. *Australian Honeyeaters*. The Bird Observers Club, Melbourne.
- Päckert, M. 2018. Song: the learned language of three major bird clades. In *Bird species: how they arise, modify and vanish*. D. T. Tietze (ed). Springer Open <http://doi.org/10.1007/978-3-319-91689-7> pp 75-94.
- Pizzey, G., Knight, F. and Pizzey, S. 2012. *The Field Guide to the birds of Australia*. 9th ed. Harper Collins, Sydney.
- Price, T. 2008. *Speciation in birds*. Roberts and Co., Greenwood Village, CO, USA.

Schodde, R. and Mason, I. J. 1999. *The directory of Australian birds*. CSIRO Publishing, Collingwood, Victoria.

Simpson, K. and Day, N. 2004. *Field guide to the birds of Australia*. 7th ed. Penguin Group Camberwell, Victoria.

Slater, P. 2009. *The Slater field guide to Australian birds. Second Edition*. Reed New Holland, Sydney.

Stewart, D. 2018. The David Stewart Wildlife Sound Collection. Albany Creek, Queensland.

White, S. A. 1913. Field ornithology in South Australia. In the mallee. *Emu* 12: 179-185.

Andrew Black,
South Australian Museum,
North Terrace, Adelaide 5000 SA
abblack@bigpond.com

David Stewart,
Albany Creek 4035 QLD
davidstewart@naturesound.com.au