Are there two species of Graceful Honeyeater in Australia?

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Abstract. Two subspecies of Graceful Honeyeater *Meliphaga (Microptilotis) gracilis* are recognised in north-eastern Queensland: *imitatrix* inhabiting the Wet Tropics and *gracilis* inhabiting northern Cape York Peninsula. Vocalisations differ greatly between the two, so the strong possibility emerges that they are distinct species. The ranges of these taxa are separated by ~140 km in the vicinity of Cape Flattery–Princess Charlotte Bay on the eastern coast of Cape York Peninsula. Significantly, a thorough search confirms that there have been no specimens collected from this geographical gap between the two populations and previously suspected intergradation does not occur. This paper describes the considerable differences between the two, especially with respect to vocalisations, and suggests that these taxa represent distinct species.

Introduction

Approximately 16 species of yellow-eared honeyeaters (Meliphagidae) of New Guinea and Australia have long been assigned to one genus, Meliphaga. Renowned for their extraordinarily similar plumage patterns and difficulty of field identification, some New Guinean forms (often called the mimic honeyeaters) are barely distinguishable from one another even in the hand. Others, however, are readily distinguished by size and vocalisations (e.g. Lewin's Honeyeater M. lewinii of eastern Australia). Three molecular phylogenetic analyses (Norman et al. 2007; Joseph et al. 2014; Marki et al. 2017) all showed that a deep divergence separates two subgroups within Meliphaga. The two subgroups diverged from each other c. 10 million years ago, a divergence time as old or older than many familiar, uncontested generic distinctions elsewhere among honeyeaters. Generic or certainly subgeneric distinction seems warranted for the two groups. This paper concerns a case for recognising yet another suite of subtle distinctions within one of the currently accepted Microptilotis subgroup of species, the Graceful Honeyeater hereafter referred to as Meliphaga (Microptilotis) gracilis. Two taxa are currently recognised in this species: M. g. imitatrix (Mathews, 1912) mostly confined to the Wet Tropics of Queensland, and M. g. gracilis (Gould, 1866) inhabiting northern Cape York Peninsula and islands of the Torres Strait with an extralimital range including southern New Guinea and the Aru Islands (Schodde & Mason 1999; Higgins et al. 2001; Beehler & Pratt 2016; IOC 2017).

The subspecies *imitatrix* (hereafter *imitatrix* for simplicity) is confined to a narrow strip east of the Great Dividing Range, from about Mount Webb National Park (15°04'S, 145°08'E) in the north, to south of Ingham (18°39'S, 146°10'E) in the south. It is mostly uncommon about the northern extremity of its range, i.e. about Cooktown and northwards (LN pers. obs.; McLean 1995; K. Shurcliff pers. comm.) and becomes rare south of Ingham at the southern extremity (LN pers. obs.; Garnett & Cox 1988; Wieneke 2010). On the Australian mainland, the subspecies *gracilis* (hereafter *gracilis* for simplicity) occurs from the tip of Cape York Peninsula southwards on the eastern coast to the vicinity of Annie River in the north-western corner of Rinyirru (Lakefield) National Park (CYPAL) (14°39'S,

143°51′E) and the nearby lower reaches of Saltwater Creek (14°42′S, 143°51′E). A specimen (ANWC B14452) in the Australian National Wildlife Collection, Canberra, was collected from a small isolated area of semi-deciduous vine forest in western Bathurst Bay, 50 km north-east of Saltwater Creek (14°18′S, 144°17′E; see Distribution below). On the western coast of Cape York Peninsula, *gracilis* extends southwards to at least Pormpuraaw (Edward River) (14°54′S, 141°37′E) (Figure 1).

Schodde & Mason (1999) suggested that a zone of intergradation exists between *imitatrix* and *gracilis* in the area south of Cape Melville. This area is mostly difficult to access. Schodde & Mason (1999, p. 262) remarked that

the two forms in Australia intergrade rather abruptly at the ... Torresian Barrier ... between the Endeavour and Bloomfield Rivers, northeast Qld. The pattern of differentiation, both morphological and geographical, parallels that in *M. notata* [Yellow-spotted Honeyeater *Meliphaga notata*] (Gould) precisely; both species occur in the same habitat over the same range in Australia. Even so, the identity of populations, if present, between Cooktown and Princess Charlotte Bay still needs resolution.

Both subspecies mostly inhabit rainforest: *imitatrix* in lowland rainforest especially edges of rainforest, adjacent more open forest and parks and gardens to an altitude of ~500 m; *gracilis* in lowland rainforest, gallery forest and semi-deciduous vine forest including areas where vine scrub and rainforest are confined to small isolated coastal pockets (LN pers. obs.; Higgins *et al.* 2001). Neither inhabits the extensive drier open tropical woodlands covering much of Cape York Peninsula and to the west of the Wet Tropics.

In the field, the two forms are superficially similar but with a few subtle differences: overall *gracilis* appears slightly more yellowish than *imitatrix*, which appears darker and more olive-green. The simple single *plick* call of *imitatrix* is a feature of lowland Wet Tropics rainforest (see Results). The much more complex vocalisations of *gracilis* of northern Cape York Peninsula are strikingly different, however. Although *imitatrix* is restricted to two distinct vocalisations, I have recorded no fewer than 12 different vocalisations, including song, for *gracilis*. Although *gracilis* has song, *imitatrix* appears to have no recognisable song. This paper documents my attempts to study and assess

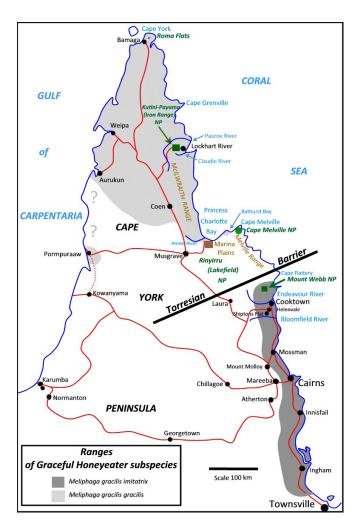


Figure 1. Distribution of Graceful Honeyeater subspecies in northern Queensland. NP = National Park.

taxonomic significance of the different vocalisations of *imitatrix* and *gracilis*.

Methods

Fieldwork

From 1995 to late 2017, I undertook fieldwork from the tip of Cape York Peninsula, Roma Flats, Lockerbie Scrub and Bamaga southwards to Townsville and westwards to the western coast of Cape York Peninsula (Weipa, Pormpuraaw, Kowanyama) and eastwards to the eastern coastline to cover the Wet Tropics and Cape York Peninsula bioregions. No fewer than 40 trips, mostly of 5–7 days' duration, were undertaken, always camping out remotely in the bush. Although this fieldwork covered the avifauna of each bioregion, every opportunity was taken to study the Graceful Honeyeater once it became apparent that two very different populations exist.

Sound recording

From 2009, I recorded vocalisations in WAV format using a Sennheiser ME66 directional microphone and an Edirol R-09 recorder. Recordings were made over many locations, generally throughout the ranges of both forms, especially throughout the range of *gracilis* on Cape York Peninsula and mostly in the northern range of *imitatrix*. Spectrograms have been made from these recordings using Raven Light v. 2.00, with FFT512. Playback on an Olympus LS-10 recorder with a Mineroff SME-AFS amplified field speaker was used to determine responses by individuals of one form to the vocalisations of the other.

Photographs

Numerous photographs of both forms were taken, using call-playback, an alarm call of *gracilis*, and an extremely rare vocalisation of *imitatrix* to attract birds within photographic range. Only photographs with birds behaving naturally were used. Earspot shape and gape colour were then analysed on computer from the photographic images. This proved to be very consistent and the most accurate method to distinguish the two forms. Museum specimens were not used to determine shape of earspot because of extreme distortion of the shape during skin preparation. Similarly, determining this from captured birds was avoided as the earspot can be altered by a bird under stress. Gape colour was easily determined with the same method.

Eye colour was analysed in similar fashion by increasing the size of a photograph of the eye on computer. In some instances, eye colour could be determined in the field with the aid of Canon 15×50 image-stabilised binoculars when sunlight was shining directly into the eye.

Locality records—specimens, Atlas, other observers

I searched databases of skin specimen collections held in the Australian Museum, Museums Victoria, Queensland Museum, South Australian Museum, and the Australian National Wildlife Collection – CSIRO. Records were also obtained from herpetologists (e.g. C. Hoskin, James Cook University) who have worked in higher parts of the Melville Range. I examined records of birds from relevant Queensland national parks published by the Queensland Government Department of Environment and Science.

The Atlas of Living Australia database (https://www.ala. org.au/) was checked but only one record was found from the critical gap between Mount Webb National Park and Saltwater Creek. There are a further 10 records from an area in southern and western Rinyirru (Lakefield) National Park (CYPAL), between Laura and Musgrave, close to the main Peninsula Developmental Road. However, these records are highly likely to be misidentifications, probably of the Brown Honeyeater Lichmera indistincta which is very common throughout this entire area. Both forms of Graceful Honeyeater are mostly rainforest inhabitants. However, this entire area is either dry, very open mixed woodland dominated by mainly Darwin Stringybark Eucalyptus tetrodonta, or low grassy open Broad-leaved Paperbark Melaleuca viridiflora woodland, neither of which is inhabited by the Graceful Honeyeater. Moreover, this is an area in which I have spent much time over a period of 26 years and at no time have I recorded the Graceful Honeyeater there, nor would I expect to. The record from the gap between Mount Webb National Park and Rinyirru (Lakefield) National Park (CYPAL) is also from entirely unsuitable habitat consisting of areas of low grassy open Broad-leaved Paperbark woodland interspersed with saline tidal mudflats.

Identifying Graceful, Yellow-spotted and Lewin's Honeyeaters without vocalisations being heard is nearly impossible for those unfamiliar or only partly familiar with these difficult species. For example, in the Atlas of Living Australia, the Graceful Honeyeater, a lowland species, is often recorded from Mount Lewis [>1000 m above sealevel (asl)] ($16^{\circ}35'S$, $145^{\circ}17'E$) and a few areas across the Atherton Tableland (700-1100 m asl). It is well-known amongst local birders (also LN pers. obs.) that only Lewin's Honeyeater exists at these high altitudes.

Results

Distribution

I observed no Graceful Honeyeaters in a wide gap between the ranges of the forms north and south of Cape Melville (Figure 1) and therefore no evidence of intergradation between imitatrix and gracilis (contra Schodde & Mason 1999). The range of *imitatrix* extends further north than the Endeavour River to about Mount Webb National Park, ~50 km north of Cooktown, where it occurs sparingly in lowland rainforest. The southernmost point in the range of gracilis appears to be in the north-eastern corner of Rinyirru (Lakefield) National Park (CYPAL), close to Marina Plains and the Annie River and the lower reaches of Saltwater Creek, a point ~140 km north-west of Mount Webb National Park. A substantial portion of the area between these two points contains very open habitat, mostly on an extensive area of floodplains, as well as open tropical woodland, all of which must serve as a natural barrier. Within this gap in range of the two forms lies Cape Melville National Park (CYPAL), which contains an area of coastal scrubby monsoon-type rainforest in the lowlands, and taller, wetter rainforest on higher areas of the Melville Range (to 610 m asl), most of which is suitable habitat for the Graceful Honeyeater. However, this habitat supports a large population of the Yellow-spotted Honeyeater, which has an overall similar but continuous distribution to that of the Graceful Honeyeater throughout Cape York Peninsula, and its two subspecies (M. n. notata and M. n. mixta) probably do intergrade either north or south of Cape Melville National Park (CYPAL).

Although I have thoroughly investigated the low coastal vegetation within Cape Melville National Park (CYPAL) and adjacent areas, I have been unable to investigate the isolated higher areas of the Melville Range where a few relatively small areas of tropical rainforest stand among fields of granite boulders. Access to the higher range is difficult and usually only possible by helicopter. Because of its remoteness and difficulty of access, few data are available for this rainforest. It is extremely unlikely that an isolated population of the Graceful Honeyeater would exist in this scattered rainforest. However, researchers studying frogs and reptiles on the higher range have also compiled accurate bird lists, and the Graceful Honeyeater has not been recorded. Conrad Hoskin (pers. comm.), who has visited the higher areas on several occasions while surveying vertebrates (for James Cook University, Cairns Campus) states,

I checked my field notes for all trips and sites at Cape Melville. I am careful to record all birds I see or hear at each site and Graceful Honeyeater never appears in my notes for Cape Melville sites. Yellow-spotted Honeyeater and Dusky Honeyeater [*Myzomela obscura*] were recorded at nearly every site. I know the Graceful call well, so I would have detected it. Most of my efforts have been in the higher areas.

The Graceful Honeyeater is not on the official bird list for the Cape Melville National Park (CYPAL) published by Queensland Government (2018).

A search of databases of skin specimen collections confirms the absence of specimens collected between Helenvale (Shiptons Flat) and an area south-west of Coen, a distance of ~300 km, supporting the existence of a large distributional gap between the two forms. An isolated record from Bathurst Bay (specimen B14452 in the Australian National Wildlife Collection), if accurate, would be well within the range of *gracilis* but L. Joseph (ANWC, pers. comm.) affirms that this specimen is actually a juvenile Yellow-tinted Honeyeater *Ptilotula flavescens*.

My fieldwork, including a recheck in December 2017, indicates that birds at the northern extremity of the range of *imitatrix*, i.e. between the Bloomfield River and Mount Webb National Park, are typical *imitatrix* both morphologically and in vocalisations. Furthermore, when the rare vocalisation of *imitatrix* (see Figure 7o in 'Vocalisations recorded' section below) is played, these birds react similarly to others throughout the range of this form.

Visual differences

Both forms of the Graceful Honeyeater are generally similar in plumage but *gracilis* appears slightly more yellowish but with the belly and undertail-coverts a noticeably paler offwhite to pale olive-grey (Figures 2–3). Overall, *imitatrix* is a more uniform, darker olive-green bird with a darker forehead, crown and nape and more uniform darker greyish-olive underparts (Figures 4–5).

Rand (1936) examined specimens collected during the Archbold Expeditions and from other sources during the late 1920s and early 1930s. Twenty-seven specimens of *gracilis* collected from northern Cape York Peninsula and 19 specimens of *imitatrix* collected in the region of Cairns were examined. Rand (1936, pp. 19–20) commented on *imitatrix*:



Figure 2. Graceful Honeyeater *Meliphaga gracilis gracilis*, Pascoe River, Cape York Peninsula, northern Queensland. Photo: Lloyd Nielsen



Figure 3. Graceful Honeyeater (*gracilis*), Pascoe River, Cape York Peninsula, northern Queensland, showing offwhite belly and undertail-coverts. Photo: Lloyd Nielsen

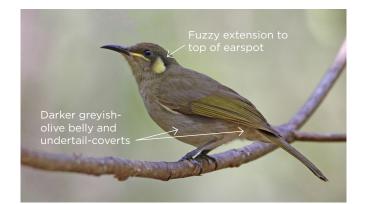


Figure 4. Graceful Honeyeater *Meliphaga gracilis imitatrix*, Mount Molloy, Wet Tropics, north-eastern Queensland. Photo: Lloyd Nielsen

....it is a recognisable form, easily distinguished from *gracilis* by the much darker under parts, the darker upper parts and the more ochraceous, less yellowish under wing-coverts, especially near the bend of the wing.

There is a slight but consistent difference in the shape of the earspot: very round in *gracilis* (Figure 6), whereas in *imitatrix* there is a small, less intense rather fuzzy yellow extension at the top of a round spot (Figure 5), which appears slightly more elongated, oblong or even wedgeshaped than in *gracilis*. Photographing birds in a natural position and later determining shape on computer monitor proved to be accurate in determining earspot shape. This was consistent in every case and can be clearly seen in Figures 5–6. Experience with this method showed that one could easily determine and note the difference in the field.

Colour of the iris also differs, being dark brown in *gracilis* and navy blue in adult *imitatrix* [brown in juvenile *imitatrix* but by the commencement of the next breeding season (September) all birds appear to have the navy-blue iris

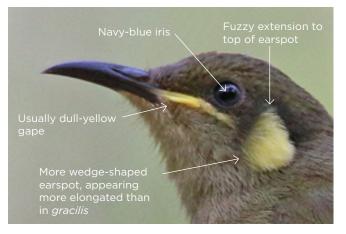


Figure 5. Graceful Honeyeater (*imitatrix*), Mount Molloy, Wet Tropics, north-eastern Queensland. The earspot in this form is less intensely coloured, somewhat diffuse yellow, and more wedge-shaped (and often appears slightly more elongated or oblong because of its anterior extension) than in *gracilis*. Note also the usually duller-yellow gape and navy-blue iris. Photo: Lloyd Nielsen

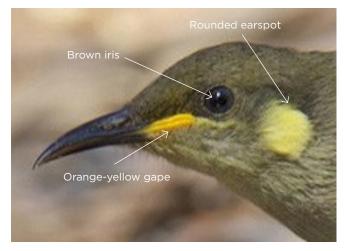


Figure 6. Graceful Honeyeater (*gracilis*), Pormpuraaw, Cape York Peninsula, northern Queensland, showing this form's typically round earspot, consistently orange-yellow gape, and brown iris. Photo: Lloyd Nielsen

colour]. The fleshy gape is consistently orange-yellow in *gracilis* (Figure 6). In *imitatrix,* a few birds (probably males) have a similar orange-yellow gape, but in most it is a noticeably paler mid yellow (Figure 5). Both forms have the diagnostic pale yellowish streak down the belly that separates Graceful from both Yellow-spotted and Lewin's Honeyeaters.

Vocalisations recorded

Twelve spectrograms for *gracilis* and three for *imitatrix* are presented in Figure 7. Letters below relate to individual spectrograms in Figure 7.

gracilis

- a. Long low piping (most common); song [Annie River, north-eastern Rinyirru (Lakefield) National Park (CYPAL)].
- b. Fast higher piping. Common (Coen).
- c. Single *plick* usually mixed with piping and other

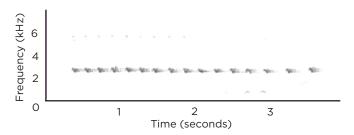


Figure 7a. Graceful Honeyeater (*gracilis*). Long low piping (most common); song.

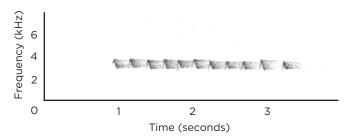


Figure 7b. Graceful Honeyeater (*gracilis*). Fast higher piping; common.

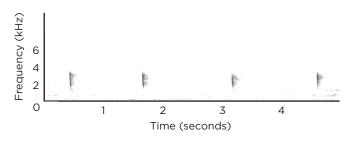


Figure 7c. Graceful Honeyeater (gracilis). Single plick.

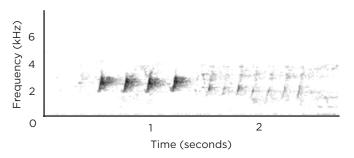


Figure 7d. Graceful Honeyeater (*gracilis*). *Whit-whit-whit* and a faster *chew-chew-chew*.

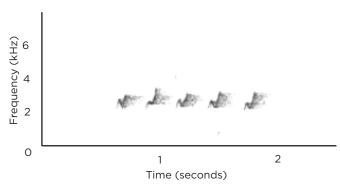


Figure 7e. Graceful Honeyeater (*gracilis*). Piping with slight upslur.

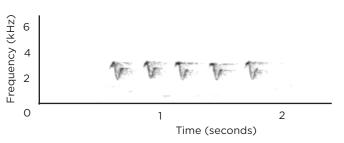


Figure 7f. Graceful Honeyeater (gracilis). Fast piping chweet-chweet-chweet...

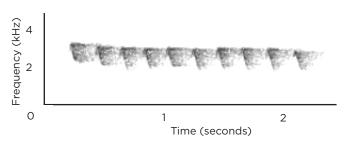


Figure 7g. Graceful Honeyeater (*gracilis*). Fast, strong slightly downslurred piping.

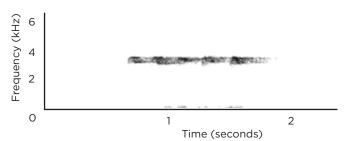


Figure 7h. Graceful Honeyeater (gracilis). Shorter very high piping.

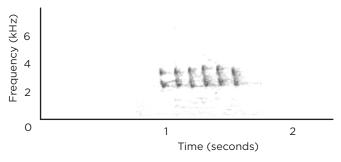


Figure 7i. Graceful Honeyeater (*gracilis*). Short, fast, rattled chatter.

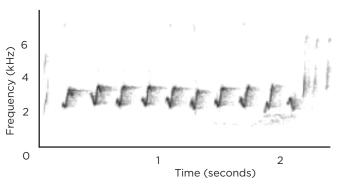
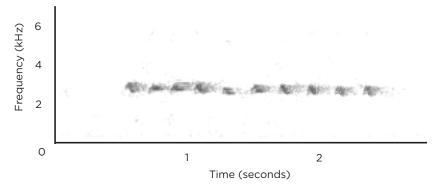
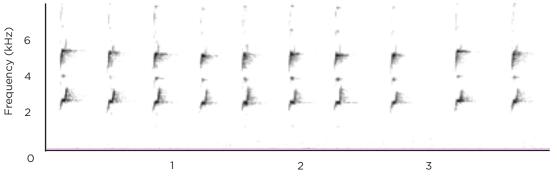


Figure 7j. Graceful Honeyeater (*gracilis*). High piping ending in a softer chatter.







Time (seconds)

Figure 71. Graceful Honeyeater (gracilis). Alarm calls.

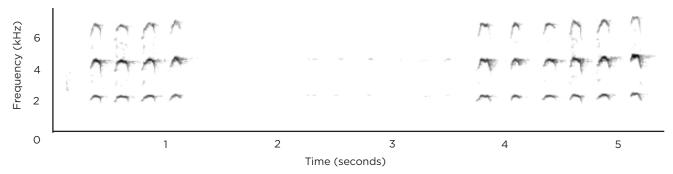
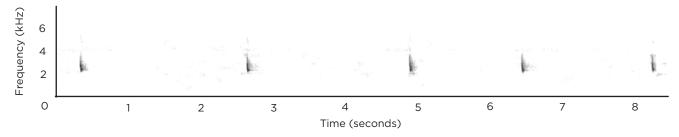


Figure 7m. Graceful Honeyeater (imitatrix). High-pitched squeaking.





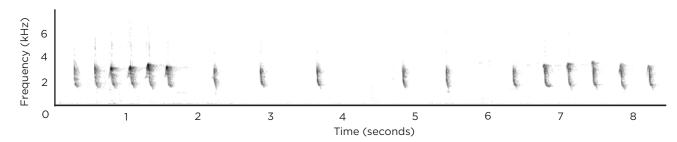


Figure 70. Graceful Honeyeater (imitatrix). Rare choup-choup-choup...

vocalisations. Uttered less than piping [Annie River, north-eastern Rinyirru (Lakefield) National Park (CYPAL)].

- d. *whit-whit...* and a faster *chew-chew-chew...* (Pascoe River).
- e. Piping with slight upslur [Kutini-Payamu (Iron Range) National Park (CYPAL)].
- f. Fast, almost double-noted piping *chweet-chweetchweet...* (Coen).
- g. Fast, strong, slightly downslurred piping (Claudie River).
- h. Shorter very high piping of ~5–6 notes (Claudie River).
- i. Short, fast, rattled chatter [Annie River, north-eastern Rinyirru (Lakefield) National Park (CYPAL)].
- j. High, longer piping of 10–12 notes ending in a softer chatter (Claudie River).
- k. Fast, slightly higher, shorter-noted piping (Running Creek near Port Stewart).
- Alarm call (two birds). Graceful Honeyeaters were attracted to this call (Kutini-Payamu (Iron Range) National Park (CYPAL)].

I did not record a series of notes, similar to the single *tchuit* of the Cicadabird *Edolisoma tenuirostris*, that were uttered uncommonly.

imitatrix

- m. High-pitched squeaking of ~4-8 notes (Mount Molloy).
- n. The common plick (Cairns).
- Rare—only briefly uttered at the beginning of the breeding season: *choup-choup-choup...* (Mount Molloy).

Notes on vocalisations

The southern form *imitatrix* utters two vocalisations: the commonly heard single *plick* (Figure 7n), seemingly used as a contact call; and a high-pitched squeaking (Figure 7m), which is uttered less often and is never heard within the range of *gracilis*. The latter vaguely resembles the piping calls of *gracilis* but differs significantly in that it is faster and much higher in pitch. It seems to be used mostly when a bird is agitated.

Only heard at the beginning of the breeding season (c. September) in *imitatrix*, though extremely rarely, is a short, unusual series of non-musical, often irregular notes (Figure 7o), somewhat reminiscent of one of the rhythmic piping vocalisations of *gracilis* but significantly lower in pitch. It is sometimes accompanied by a few irregular notes but is in stark contrast with the higher-pitched, morestructured, common piping vocalisations of *gracilis*.

In contrast with the simple vocalisations of *imitatrix*, the repertoire of *gracilis* is complex, with no fewer than 12 different and distinct vocalisations, including the single *plick*, the most common being a long low piping, which seems to be song (Figure 7a). Generally, most of these vocalisations can he heard in any small area of suitable habitat.

The single *plick* (Figure 7c) of *gracilis* is not uttered as frequently as the piping vocalisations and appears to be used mostly as a contact call. In *imitatrix*, the single *plick* (Figure 7n) is slightly shorter, sharper and slightly higher in pitch than in *gracilis*. The single note is common to several related species in New Guinea (Diamond 1972; Beehler 1978; Pratt & Beehler 2015).

The possibility that another taxon (i.e. *imitatrix*) was also present within the range of *gracilis* (one uttering the single *plick*, the other the more-complex vocalisations) was explored briefly, but it was established that all vocalisations were uttered by *gracilis* individuals. However, on one occasion, I listened and watched a bird in Kutini-Payamu (Iron Range) National Park (CYPAL) utter the single *plick* for 4 minutes without uttering another vocalisation, which was unusual; this bird proved to be a *gracilis*.

Song

Although song is evident in *gracilis*, I have never heard vocalisations that I can identify as song in *imitatrix*. Originally, it seemed that the vocalisation displayed in Figure 7o might have been an attempt at song but, from the sometimes aggressive reaction to call-playback, apparently it is not. There is a possibility that the high-pitched squeaking (Figure 7m) may be song but this squeaking seems to be uttered more when a bird is agitated. When I used the recording in Figure 7o as playback, birds uttered the call in Figure 7m more frequently as they perched between flying back and forth in response. It has been suggested that some of the New Guinean species of the genus may not have song (Diamond 1972; Gregory 2017).

Response to call-playback

I have used call-playback in many parts of the ranges of both forms of the Graceful Honeyeater primarily to test the reaction of one form to the vocalisations of the other, with the results clearly demonstrating that neither form reacts to any vocalisations of the other. To date, it has been found that birds react only to mostly one vocalisation of their own form, i.e. the alarm call (Figure 7I) in *gracilis* and the rare *choup-choup-choup* vocalisation (Figure 7o) in *imitatrix*.

When the alarm call of *gracilis* (Figure 7I) was played within its range, birds reacted casually: attracted to the source, they remained for a few minutes, usually moving from branch to branch inquisitively, and then moved away.

There was usually little reaction by *imitatrix* to either of its own vocalisations (Figures 7m–n). However, when the rare *choup-choup* vocalisation (Figure 7o) was played, reaction was generally strong and immediate, with several birds swiftly drawn to it. Often birds became agitated to the extent that some vigorous chasing back and forth occurred, mostly between two birds, sometimes three. On one occasion, in response, one bird squatted on a branch and extended its wings horizontally for *c*. 10 seconds, remaining nearly motionless all the while.

Considering the strong reaction by *imitatrix* to its own rare vocalisation, reaction by *gracilis* to this vocalisation was explored. This has been played in many parts in the range of *gracilis* and, on every occasion, it has been completely ignored.

Discussion

Among natural populations, voice is crucial in species recognition (Alström & Ranfft 2003). Voice can separate and define superficially similar species (Baptista & Kroodsma 2001). In recent years, vocalisations have played an important role in recognition of cryptic species and in turn many taxonomic revisions (Lanyon 1978; Alström & Ranfft 2003). In Australia, examples of the recognition of two cryptically similar species based largely on differentiation in voice are Bassian Thrush Zoothera lunulata and Russet-tailed Thrush Z. heinei (Ford 1983); Chirruping Wedgebill Psophodes cristatus and Chiming Wedgebill P. occidentalis (Ford & Parker 1973), and Kimberley Honeyeater Meliphaga fordiana and Whitelined Honeyeater M. albilineata (Norman et al. 2007; Miller & Wagner 2014, 2015). Extralimital examples include Oriental Cuckoo Cuculus optatus and Himalayan Cuckoo C. saturatus (King 2005; Xia et al. 2016), and Rinjani Scops Owl Otus jolandae and Moluccan Scops Owl O. magicus (Sangster et al. 2013). All were initially recognised as representing distinct species because of distinctly differing vocalisations. Many others have been recognised and separated on the same basis in other parts of the world.

In Australia, vocalisations that distinctly separate the three recognised species of yellow-eared honeyeaters are the most accurate means of field identification of each. However, in New Guinea, there are at least 10 species of yellow-eared honeyeaters, all very similar, and some are difficult to separate in the field. Some vocalisations are shared among species, despite slight differences, whereas other calls are diagnostic to a given species (Pratt & Beehler 2015).

Although authentic calls of *M. g. gracilis* from New Guinea seem to be few, one recorded by Bas van Balen from Anana Pare, Freeport, West Papua (xeno-canto record XC140379, https://www.xeno-canto.org/140379) is the *plick* call. It is almost identical with the *plick* call of *gracilis* from Cape York Peninsula, of a similar tone but slightly coarser and stronger. It is lower in pitch than that of *M. g. imitatrix*.

Although my findings are based on field-based study of vocalisations and morphological traits, Peñalba *et al.* (2017) found that the divergence of the Cape York form (*gracilis*) from the Wet Tropics form (*imitatrix*) was substantial at 1.88% mitochondrial DNA and 1.1% for autosomal markers.

Possible intergradation

Schodde & Mason (1999) examined three specimens apparently collected close to the Torresian Barrier (probably three of a total of five birds collected at Shiptons Flat, south of Helenvale) and close to the edge of the northern range of *imitatrix*. They suggested that these specimens showed some intergradation between the two forms, although no explanation or details were given. Higgins *et al.* (2001, p. 709) when commenting on this statement made the following observation "...but little material to corroborate this; one adult female (QM) from Shiptons Flat, S of Cooktown, more closely resembles *imitatrix*". I have examined photographs of the three specimens from Shiptons Flat in the CSIRO National Wildlife Collection; these specimens are all typical *imitatrix*, showing no evidence of intergradation.

Intergradation is not supported by my field observation and, considering the wide gap in ranges of the two forms, I conclude that it does not occur. One would assume that any sign of intergradation should be evidenced by paling of the belly and undertail-coverts, shape of the earspot, depth of colour of the gape and perhaps vocalisations. There is no evidence of this.

Fieldwork indicates that birds at the northern extremity of the range of *imitatrix* (i.e. between the Bloomfield River and Mount Webb National Park) are typical *imitatrix* both morphologically and in vocalisations.

Conclusions

The northern form of Meliphaga (Microptilotis) gracilis demonstrates a remarkable repertoire of complex vocalisations, all of which can be heard throughout its range. Indeed few, if any, Australian honeyeaters, especially within the smaller species of Meliphagidae, demonstrate such a range of vocalisations, including song, over such a relatively small distribution than in this taxon. Its Wet Tropics congener has only two simple vocalisations and possibly no song, resulting in a very wide difference in vocalisations between the two, and no reaction to each other's vocalisations. Recent literature has used this level (or less) of differentiation between vocalisations of two taxa in both passerines and non-passerines to argue for elevation of each taxon to species rank. I conclude that the two subspecies of the Graceful Honeyeater should be recognised as distinct species. Assessment of the widespread southern New Guinean populations remains the next piece of the story to investigate but they are currently treated as gracilis.

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