

TAXONOMIC REVIEW

Notes on the taxonomy of Cream-throated White-eye *Zosterops atriceps* and the biogeography of the Northern Moluccas

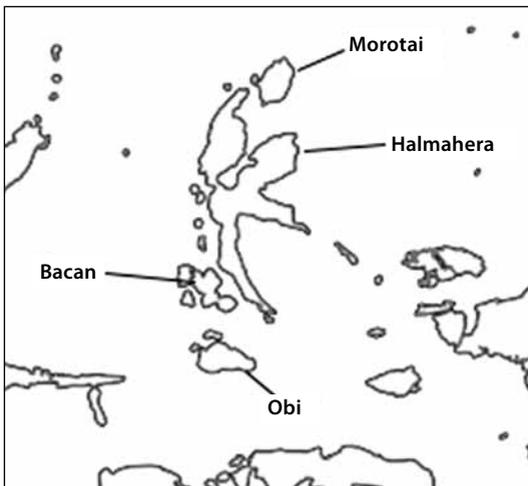
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The genus *Zosterops* has famously been described as the ‘great avian speciator’ (Diamond *et al.* 1976, Moyle *et al.* 2009) and has diversified across the Australasian and Indo-African regions into nearly 100 species (del Hoyo & Collar 2016) over, in evolutionary terms, a relatively short period of time. The Indonesian Archipelago is particularly rich in *Zosterops* diversity, with about 26 species (Eaton *et al.* 2016). However, the genus is also infamous for conservative plumage colouration occurring in a mosaic-like fashion that sees certain colour patterns variably displayed by different species across the archipelago. *Zosterops* plumage has therefore been thought of as a ‘variation on a theme’, with widely separated species often sporting an almost identical appearance, either of a yellow-bellied or grey-bellied plumage type. This *Zosterops* plumage mosaic has led to great uncertainty in the taxonomic delimitation of species. In fact, recent molecular work has shown that various traditional common names in Asian white-eye taxonomy have been wrongly delimited for decades and will require reclassification (Round *et al.* 2017, Lim *et al.* 2018).

The Cream-throated White-eye *Zosterops atriceps* complex from the Northern Moluccas

comprises three described subspecies and an undescribed population, and is one that has been associated with taxonomic upheaval in the last few years. Its cream-white throat colouration is rather unusual (albeit not unique) in this typically yellow-throated genus. On account of this trait, the Cream-throated White-eye has long been treated as a species distinct from what appear to be its closest relatives in the Central Moluccas (Seram, Buru) and Sulawesi (White & Bruce 1986, Coates & Bishop 1997). However, field observations in the Northern Moluccas in recent years have created an awareness that intra-specific variation in Cream-throated White-eyes is more pronounced than previously thought, leading to new taxonomic arrangements. Eaton *et al.* (2016) split the Cream-throated White-eye into four constituent species, a treatment acknowledged, although not entirely followed, by del Hoyo & Collar (2016), who retained the Cream-throated White-eye as a single species but recognised that the three described subspecies (Morotai *Z. a. dehaani*, Halmahera *Z. a. fuscifrons* and Bacan *Z. a. atriceps* White-eyes) may warrant species status. Here we outline our taxonomic rationale for splitting the complex into the four species recognised by Eaton *et al.* (2016), in the hope that it may lead to a more widespread adoption of this treatment.

Figure 1. Map showing the relative positions of the four main Northern Moluccan islands.



Phenotypic diversity

With the historical focus having been on the nominate form *atriceps* from Bacan and *fuscifrons* from the large island of Halmahera, earlier researchers may not have been fully aware of the true variation in plumage colouration found in the four separable populations of the complex. The most distinctive plumage is displayed by *dehaani* from Morotai (Plate 1), and anyone lucky enough to see this bird in the field will immediately wonder how this taxon could ever have been merged with any other *Zosterops* species. Its plumage is reminiscent of a North American vireo, with oversized white spectacles and loreal area on the background of a completely greyish-black head. The nearly complete lack of greenish colouration on its anterior body parts makes it one of the



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Plate 1. Morotai White-eye *Zosterops dehaani*, Morotai, Northern Moluccas, Indonesia, 15 September 2016.

most distinctive white-eyes of the Indonesian Archipelago.

The other three forms also show morphological differences that are often greater than those between many firmly recognised white-eye species, an important criterion when applying the ‘yardstick approach’ that can guide us on whether or not two allopatric forms deserve species status (Mayr & Ashlock 1991). In this respect, *fuscifrons* from Halmahera has the least conspicuous, greyest eye-ring of the four taxa, but uniquely a complete lack of grey colouration on its bright olive upperparts (Plate 2). The nominate *atriceps* from Bacan (Plate 3) has a contrastingly grey nape that is not seen in any other Asian white-eye population. On the more distant island of Obi, an undescribed form (Plate 4), previously subsumed in *atriceps*, most closely resembles *fuscifrons* but has the thinnest, most crisply white eye-ring and most extensive yellow lower mandible of all the forms. In addition, there are minor differences in the hue of colouration on other plumage parts. Field research into these four distinct forms was previously hampered by the difficulties in reaching Obi, Morotai and Bacan, but with improvements in ferry and air services access is now far easier and consequently our knowledge of these taxa has improved.

Bioacoustic differentiation

Until recently, only the vocalisations of *fuscifrons* were known, thus bioacoustic comparison was not possible. We were able to obtain sound recordings of the three remaining populations during visits to the islands between 2014 and 2017 and confirm that the characteristic dawn songs of this genus, and delivered by each of the four taxa, are very distinctive. Minor variations in calls also seem to exist, although at least Bacan, Morotai and Halmahera White-eyes seem to give a homologous soft *tip*, *twit* and *pip* respectively, while Bacan and Obi White-eyes have been recorded uttering homologous series transcribed as *wee-wee-wee...* and *peep-peep-peep...* respectively.

The two most differentiated and outstanding songs are those of the Obi and Morotai populations. The Morotai song contains full-throated musical warbles interspersed with characteristic monotonous, high-pitched series of *twee-twee-twee* or *ti'ti'tit'wititwititwitititit* notes, lasting 2–4 sec. The Obi song is a long, unmistakable winding series of sweet musical, predominantly down-slurred notes, roughly sounding like *tew-wit-tew-tew-tewwit-tew-tew-wit...*, lasting 4–10 sec. The Halmahera and Bacan songs are relatively similar to each other, both being rather short



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Plate 2. Halmahera White-eye *Zosterops fuscifrons*, Halmahera, Northern Moluccas, 6 December 2014.

Plate 3. Bacan White-eye *Zosterops atriceps*, Bacan, Northern Moluccas, 10 September 2016.



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Plate 4. Obi White-eye *Zosterops* sp. nov., Obi, Northern Moluccas, 13 September 2016.

series of undulating, sweet musical notes lasting only 1–2 sec. However, individual Bacan songs always terminate in a rising flourish, whereas the Halmahera birds' songs have no fixed frequency pattern and never seem to include the final flourish.

Ecological differentiation

Perhaps one of the greatest surprises arising from recent field visits to the Northern Moluccas is the realisation that the four Cream-throated White-eye forms are not ecologically similar. On Halmahera, *fuscifrons* has long been known as a fairly common inhabitant of forests at all altitudes, but the distinctive vireo-like *dehaani* from Morotai appears to be a predominantly montane and submontane bird, rare in the lowlands. During an expedition to Morotai in November 2015 that may have been one of the few ornithological field trips to venture above 800 m, FER found *dehaani* to be abundant in shorter vegetation above about 800 m. Other visitors have also reported that *dehaani* was much more common at higher altitudes (JAE pers. obs.). Similarly, the undescribed population on Obi seems to be an inhabitant of higher altitude above 390 m (Mittermeier *et al.* 2015, JAE pers. obs.). In stark contrast, nominate *atriceps* from Bacan has

had a history of escaping the attention of visitors who have focused on higher altitudes to find Bacan's endemic taxa, although it is not difficult to see in scrub a few km outside Labuha, the island's capital. Its preferred habitat is now thought to be forest edge and scrub at flat, low altitudes, and it is apparently not recorded above 700 m.

Biogeography

Although the Northern Moluccas are often thought of as a homogenous region of endemism within Wallacea, field research in recent years has discovered many cases of single-island endemism on each of the four main islands (Mittermeier *et al.* 2015, Eaton *et al.* 2016). Each is characterised by different levels of biogeographic isolation and topographical relief, making for distinct evolutionary arenas.

Although Halmahera, the largest island, is approximately seven times bigger than Obi, the next largest, it has a relatively small unique endemic element compared with similar size Wallacean islands such as Seram (Eaton *et al.* 2016). Most endemic birds that make Halmahera well-known ornithologically are shared with surrounding islands, mainly Bacan and Morotai. A principal reason for this low level of exclusive

endemism is the low-lying relief of the island, with few mountains that rise above 1,500 m.

Gn Buku Sibela (2,111 m) on Bacan is the highest peak of the Northern Moluccas and is the main reason why Bacan has a moderate level of single-island endemism, almost all of which is restricted to this mountain. However, Bacan was the only major island regularly linked to Halmahera by a narrow land bridge during glacial periods when global sea levels fell by about 120 m (Bintanja *et al.* 2005). In this respect, the realisation that nominate *atriceps* from Bacan is a lowland form was a major surprise: the underwater ridge between Bacan and Halmahera is only 5–10 m deep, so a land connection would have existed only about 12,000 years ago, at a time when Halmahera was probably already inhabited by anatomically modern humans. The great plumage differences between *fuscifrons* and *atriceps* would be inconceivable if those two forms had readily hybridised during the time in which the islands were connected, as such distinct morphological differences are usually thought to take hundreds of thousands of years, not a mere 12,000 years, to evolve (Avisé & Walker 1998). It is therefore likely that *atriceps* and *fuscifrons* behaved like members of different species during the last land connection, refraining from interbreeding despite opportunities to do so, as any substantial interbreeding would have quickly wiped out their morphological differences.

Morotai lies less than 20 km off northern Halmahera, with the channel between them reduced to a mere 5 km by falling sea levels during the most recent ice ages, but has never been linked to it during the existence of the Cream-throated White-eye. However, *dehaani* on Morotai is unlikely to have engaged much with Halmahera's *fuscifrons* during those periods because it possesses one of the most distinct white-eye morphologies, rendering unlikely any gene flow during Quaternary times. Indeed, its highland ecology would have minimised overlap with any lowland stragglers of *fuscifrons*.

Last but not least, Obi is the most isolated deep-sea island in the Northern Moluccas, permanently separated from Bacan and Halmahera by about 50 km of open sea. Consequently, its undescribed montane *Zosterops* population is unlikely to have been in contact with the other forms since its emergence. It is probably not a coincidence that this white-eye's morphological distinctions are relatively modest. Given the occasional contact that *dehaani* from Morotai and particularly *atriceps* from Bacan would have had with Halmahera *fuscifrons*, they may have been subjected to an evolutionary phenomenon called 'character

displacement', in which there is selection for two forms to adopt different phenotypes in areas of contact in order to minimise the chance of hybridisation. This character displacement may have favoured stronger differences among white-eye forms that occasionally come into contact, whereas it would be irrelevant to Obi's undescribed population that is geographically well-separated from other forms.

Taxonomic recommendations

Morotai White-eye *Zosterops dehaani*

The Morotai form is the most unequivocal split of the four Cream-throated White-eye forms. Its plumage colouration is one of the more distinctive found in the entire Australasian radiation of white-eyes, and it shows exceptional differences from the other three forms in its dawn song. Its submontane and montane habitat specialisation contrasts with the neighbouring form *fuscifrons*, which ranges commonly across the lowlands of Halmahera, thereby reducing chances for gene flow during glacial maxima when the sea level gap between Morotai and Halmahera would have been reduced to a few km.

Obi White-eye *Zosterops* sp. nov.

The yet-to-be-described white-eye population from distant Obi has perhaps the most distinctive dawn song of the four taxa and deserves species status predominantly because of this. Although morphological divergence from *fuscifrons* in Halmahera is not striking, the most pronounced differences relate to the white eye-ring, which presumably has important signalling functions in sexual selection. Being geographically distant from the other forms and with no history of land connections to any other island, there may have been a history of very limited interaction since first colonisation. Its relatively slower phenotypic divergence from *fuscifrons* may be attributable to the lack of a need to avoid hybridisation (i.e. character displacement).

Halmahera White-eye *Zosterops fuscifrons* and Bacan White-eye *Zosterops atriceps*

Genomic evidence for the relationships of Cream-throated White-eyes is not yet available but, based on morphology and bioacoustics, the forms *atriceps* and *fuscifrons* appear to be most closely related to each other. This may be unsurprising, given that regular land bridges have linked Bacan and Halmahera during glacial maxima, the last time as recently as about 12,000 years ago. Given the opportunity for gene flow during such periods, the most important taxonomic consideration is to assess whether existing

differences could have evolved over such a short time or would have already been present during their last connection.

While the songs of Morotai and Obi White-eyes are unmistakably different, at least the songs of Bacan and Halmahera White-eyes appear to be two variations on a common theme to the human ear. Nevertheless, important consistent differences in frequency modulation exist (see above). Also, the Bacan White-eye is unique in having a striking grey nape. This level of phenotypic and vocal differentiation is unlikely to have arisen within a few thousand years, a time frame during which modern human societies would have already existed in the region. Hence, we suspect that the two forms were already differentiated during the last period in which they were in contact. At the time of last contact, it is unlikely that they would have engaged in widespread interbreeding because even low levels of gene flow over a few generations are powerful in homogenising populations and wiping out differences. In summary, they would have acted as two different species during their last encounters, arguing for species level for both of them.

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